TRANSACTIONS of the AMERICAN FISHERIES SOCIETY

October 1961

VOLUME 90

NUMBER 4

Dissolved-Oxygen Requirements of Three Species of Fish[1]

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ABSTRACT

Critical dissolved-oxygen levels and standard metabolic rates were determined for the bluegill, *Lepomis macrochirus*; largemouth bass, *Micropterus salmoides*; and the channel catfish, *Ictalurus punctatus*, at 25° C., 30° C., and 35° C. Two types of experiments were conducted: shock tests in which the dissolved oxygen was dropped rapidly from near saturation to a critically low point; and acclimation tests in which the dissolved oxygen was lowered gradually over a longer period of time. The minimal dissolved oxygen survived by fish in acclimation tests was lower than that survived in shock tests at any given temperature. In shock tests the minimum dissolved oxygen survived by bluegills was 0.75 p.p.m. at 25° C., 1.00 p.p.m. at 30° C., and 1.23 p.p.m. at 35° C. Slightly higher values were obtained for the largemouth bass at all three temperatures and for the channel catfish at 25° C. and 30° C. At 35° C. the channel catfish was more tolerant of low dissolved oxygen than either the bluegill or largemouth bass. In the acclimation tests the critical oxygen values obtained for bluegills were 0.70 p.p.m. at 25° C., 0.80 p.p.m. at 30° C., and 0.90 p.p.m. at 35° C. With the exception of the channel catfish at 35° C. slightly higher values were obtained with the largemouth bass and channel catfish. Within each species there was little difference between standard metabolic rates at the three temperatures. The standard metabolic rate of the bluegill at 25° C. was lower than that of the other species at the same temperature. Bluegills and largemouth bass weighing more than 15 grams showed no change in metabolic rate with increasing size, but below this weight, metabolic rate varied inversely with weight.

INTRODUCTION

There is a large and rapidly growing literature on the respiratory physiology of fishes. (1957) has recently provided workers an excellent review of this field. Comisons of published data on the oxygen uirements of various species of fish are icult because different authors employed ying techniques. These variations are: use est fish in groups or as isolated individu- use of flowing water in an open-ended em as opposed to recirculated or standing er in a closed system; differences in the amount of activity allowed or required of test fish; differences in size of test fish; and differences in the previous thermal and dissolved-oxygen regimes of test fish. In the experiments reported here the test fish were allowed a minimum of activity so that their oxygen requirements were as near the resting or standard rate as possible. The elimination of activity as a variable results in a considerable simplification of the apparatus required and in improvement of control of other variables. Findings on the oxygen requirements of either resting or active fish under laboratory conditions are difficult to interpret in terms of conditions in nature. Recent authors who have investigated the active metabolism of fishes under various circumstances (Basu, 1959; Katz, Pritchard, and Warren, 1959) have all warned that their results cannot be directly applied to field conditions. The present authors have thus adopted the view that minimal activity conditions should be used

This investigation was begun under a research ract with the National Council for Stream Im- ement, and a portion of the results herein re- ed have appeared in mimeographed form as nical Bulletins 111 and 133 of that organization. the last 6 months of 1960 the work was sup- ed by grant G-13328 of the National Science ndation. Publication sponsored in part by the ersity of Georgia.

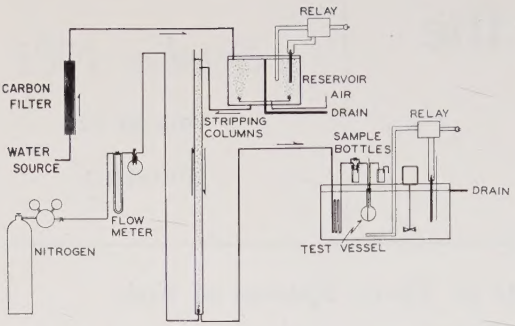


FIGURE 1.—Diagrammatic drawing of test apparatus.

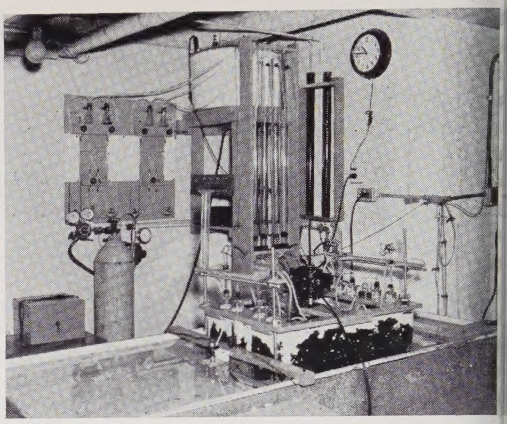


FIGURE 2.—Apparatus for maintaining control water flow, dissolved-oxygen concentration, and te perature.

when studying the fundamental interrelationships existing between the fishes' ability to survive and the various controllable environmental factors.

In nature fishes might be subjected to critically low dissolved oxygen at various rates of speed. They might be exposed to a rapid drop in dissolved oxygen due to the sudden addition of pollutant, or they might experience a more or less gradual decline in oxygen concentration. Under the latter circumstances fish might be able to mobilize their respiratory faculties and withstand lower concentrations than would otherwise be possible. Shepard (1955) has demonstrated the acclimation abilities of brook trout, *Salvelinus fontinalis*, at 10° C. The present work was designed to determine the minimal oxygen requirements and acclimation abilities of three species of fish (bluegill, *Lepomis macrochirus*; largemouth bass, *Micropterus salmoides*; and channel catfish, *Ictalurus punctatus*) at 25° C., 30° C., and 35° C. This work could then serve as a basis upon which to study the interrelationships of other environmental factors with dissolved oxygen and their effects on acclimation.

APPARATUS AND METHODS

The apparatus employed in these experiments was designed to provide a source of water in which rate of flow, temperature, and dissolved oxygen could be simultaneously controlled. It was essentially the same as that used by Van Horn[2] and Dimick.[3] A simp fied diagram of the apparatus is presented Figure 1, and a photograph of the laborato set-up is shown in Figure 2.

Four stripping columns were fed by grav with a supply of heated, aerated tap wa from the constant-head reservoir. The amou of water available was limited by the heati capacity of the electric circuits in the labo tory and was therefore dependent upon t operating temperature and the temperature the incoming tap water. Athens city wa was used for several years without additio treatment. Residual chlorine tests with a s sitivity of 0.03 p.p.m. were uniformly ne tive. In the spring of 1959, however, t residual chlorine increased to a point wh it became necessary to install activated carb filters in the water supply line. Manomet on the nitrogen lines made it possible to c brate nitrogen flows to individual colun and set them for predetermined oxygen v ues. Some difficulty was encountered maintaining constant nitrogen flows with dinary two-stage gas regulators, and it v necessary to introduce a third stage of re lation. This stage consisted of a low-press regulator of the type used to control the fl of gas to pilot lights. The stripping colun were made of pyrex tubing 2 inches in dia eter. Originally these were made 7 feet lo but were shortened to 4 feet after several als. Various types of packing materials w used in the columns, but all were discar when it was found that carborundum diffus worked satisfactorily and presented no cle ing problems. Slime growth, particularly high temperatures, made it necessary to

[2] Van Horn, W. M. (1954) Minimal oxygen requirements for certain species of fish. National Council for Stream Improvement, Tech. Bull. 66, 18 pp. (Mimeo.)

[3] Dimick, R. E. (1954) Some effects of low concentrations of dissolved oxygen on juvenile silver salmon. National Council for Stream Improvement, Tech. Bull. 68, 23 pp. (Mimeo.)

ntle and thoroughly clean the entire appa-
us after each few weeks of operation. Wa-
drawn from the bottoms of the stripping
umns passed to the constant temperature
h where the test vessels were located. Here
was run through manifolds immersed in
bath so that heat lost in passage through
exposed parts of the apparatus could be
tored. The water then passed through in-
ning sample bottles before entering the
t vessels. By-passes were provided so that
bottles could be removed without inter-
ting the flow of water. Upon leaving the
t vessels the water passed through outgoing
ple bottles before being wasted to the
h. The sample bottles had a capacity of
) milliliters. The sizes of the test vessels
ied with the size of the fish being tested.
y ranged from 250-milliliter flasks to half-
on jars. The test vessels were wrapped in
minum foil so that the fish would not dis-
b each other or be disturbed by activities
he laboratory.

n long-term experiments where respiratory
s were measured, dissolved-oxygen deter-
ations were made simultaneously on the in-
ning and outgoing sample bottles for each
vessel. Six sets of dissolved-oxygen de-
inations generally were made at evenly
ced time intervals throughout 12 hours
each day of an experiment. The rate of
er flow through the vessel was measured
he same time by measuring the volume of
flowing water for 1 minute. The rate of
w of water through the test vessels was
ied from 90 to 500 milliliters per minute
ording to the rate of oxygen consumption
he test fish. An oxygen drop of at least
p.p.m. was considered necessary in order
btain a reasonable estimate of the meta-
ic rate of the fish. However, even under
ditions of maximum water flow oxygen
ps approaching 0.5 p.p.m. were usually
ained for the larger fish tested (50 grams
larger). In some instances this amounted
half the available oxygen and there is no
bt that this limit, imposed by practical
siderations, affected the ability of test fish
survive low dissolved-oxygen concentra-
s. Fish exposed to low dissolved oxygen
ariably oriented to the incoming stream of
er and almost took the tube into their
uths. The rate of flow of water through
test vessels in all cases precluded the pos-
lity that carbon dioxide or other meta-
c wastes could accumulate in significant
unts. In short-term experiments, where fish were suddenly subjected to low dissolved oxygen, no attempt was made to estimate respiratory rate. In these experiments six or more dissolved-oxygen determinations were made per day on the incoming water, and the rate of flow of water was increased so that the dissolved oxygen drop across the test vessel was 0.1 p.p.m. or less.

In a few of the long-term experiments at higher temperatures considerable bacterial growth occurred on the inner surfaces of the test vessels and the tubes leading to them. Oxygen-consumption determinations were made of the apparatus before fish were placed in the vessels and at the termination of a given experiment. In those cases where significant bacterial oxygen consumption occurred these values were plotted on semi-log paper against time so that appropriate corrections could be interpolated for each day of the experiment. The greatest magnitude reached by such corrections was 10 percent of the respiratory rate of the test fish. The respiratory rates of the fish were calculated and expressed as milligrams of oxygen consumed per gram of fish per hour. In long-term experiments the test fish suffered some weight loss. For the purpose of calculations, daily estimates of the weight of each fish were made from semi-log plots of initial and final weights against time.

A quantitative modification of the standard Winkler procedure was used in the oxygen analyses. Tests for interfering substances were all negative. One milliliter each of manganous sulfate and alkaline iodide solution was added to each sample bottle followed by 2 milliliters of half-strength sulfuric acid. The latter modification was made to insure that the bottle was completely filled when it was stoppered for the final mixing. A 100-milliliter aliquot of each sample was titrated with 0.0125 N sodium thiosulfate. Titrations could be reproduced to within 0.02 to 0.04 p.p.m. of dissolved oxygen. Replacement of a conventional burette with one of the piston type resulted in even closer reproducibility and a considerable saving of time. Time relationships between the various steps in the determinations were maintained constant. Extended exposure to the atmosphere or excessive stirring of the iodine solution obtained in the final step was found to introduce significant error. Titrations were therefore performed immediately on each sample, and a magnetic stirrer was used only near the end of each titration. The correction recommended by Ohle (1953) to compensate for the

small amount of oxygen introduced with the Winkler reagents was not applied to our data.

Test fish

All fish were placed in holding tanks in the laboratory and supplied with running tap water when they were brought in from the field. After chlorine became a problem in the tap water, wastage from the constant head reservoir was fed into the holding tanks. This water had been passed through a carbon filter, aerated, and warmed. The time allowed for temperature acclimation depended upon the temperature of the water from which the fish were obtained and the temperature of the indoor holding tanks. Experiments at 25° C. were conducted in the cooler months of the year when outdoor pond temperatures were no lower than 8° C., while experiments at 30° C. and 35° C. were restricted to the summer months when pond temperatures were around 30° C. In general fish were held in the laboratory at gradually increasing temperatures and were maintained at the test temperature for at least 3 weeks before they were used in tests. Particular care was taken to insure temperature acclimation in tests made at 35° C. since this was so near the lethal level. Test fish to be used at 35° C. were held at this temperature for no less than 30 days. Fish were fed sufficiently to keep them in good condition, but they were not fed for at least 2 days before being used in an experiment nor during the course of an experiment. Fishes which survived one experiment were never used in any other.

The bluegills were seined from a farm pond on the USDA Piedmont Experiment Station near Watkinsville, Georgia. Some largemouth bass were obtained from the same pond as the bluegills, others were seined from Rock Eagle Lake in Putnam County, Georgia. Because they were excitable, the bass were narcotized in 3-percent sodium chloride solution when it was necessary to handle them in the laboratory. Recovery from this treatment appeared to be complete and almost immediate. Two lots of channel catfish were obtained from Dr. H. S. Swingle at Auburn University. The first lot, obtained in March 1959, was hatched in 1957 in ponds at Fort Worth, Texas, and had been held in ponds at Auburn, Alabama, since their first summer of life. The second lot, obtained in November 1959, had been hatched in ponds at Marion, Alabama, in 1957. A third lot of catfish was obtained from Mr. Jack Snow in March 1960. These fish were hatched and reared at the Mari Fisheries Station in 1959.

Experimental procedures

Two types of experiments, here designat as shock tests and acclimation tests, were cc ducted. In the shock tests, fish which h been in water saturated with air at the t temperature were suddenly subjected to w ter with critically low dissolved oxygen. T lowest dissolved-oxygen level at which fi consistently survived for 24 hours was fined as the critical oxygen level. Successi trials at various dissolved-oxygen concent tions made it possible to bracket the criti value for each species at each temperatu At first, shock tests with bluegills were p formed by stabilizing the dissolved oxygen water flowing through the test vessels at t desired level and then placing the fish the vessels. Later a more precise control the apparatus made it possible to calibrate t nitrogen manometers in advance and pla the fish in the apparatus at saturation for hours before beginning the test. The nitrog flow could then be set at the predetermin level and the test fish subjected to water w the desired dissolved oxygen within 1 to hours. This procedure gave the fish an portunity to recover from the effects of han ling before being subjected to the stress low dissolved oxygen. Without excepti handling and confinement in the test vess increased the fish's rate of oxygen consun tion for a period of at least 24 hours.

Acclimation tests were performed by pl ing a fish in each test vessel with the inflowi water saturated with air. With one fish maining at saturation to serve as a contr the others were subjected to gradually decl ing levels of dissolved oxygen in a dai stepwise fashion. These steps were large the beginning of an experiment but were creased in magnitude as critical dissolv oxygen levels were approached. Daily creases in dissolved oxygen continued until t experimental fish died. The critical dissolv oxygen value for each fish was determined the average dissolved oxygen that prevai in the inflowing water for the last 24 ho of its life. These tests required very care control of temperature, water flow, and nit gen flow over the period of the experime (11 to 15 days each). Unavoidable a sometimes inexplicable mishaps occasiona occurred which voided the results of ma experiments.

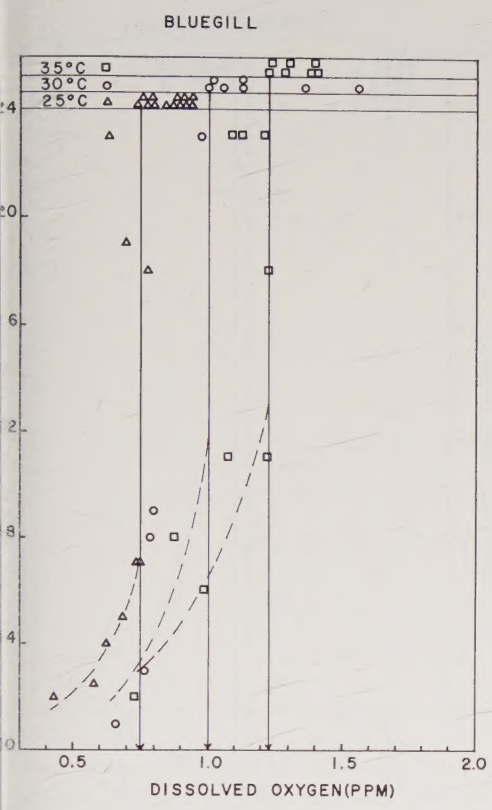


FIGURE 3.—Results of shock tests with bluegills wing survival times up to 24 hours at various dis- ved-oxygen concentrations at 25° C., 30° C., and C.

RESULTS OF SHOCK TESTS

Survival times (up to 24 hours) at the ee test temperatures and at various oxygen els are plotted for individual fish of the ee species in Figures 3, 4, and 5. The tical levels of dissolved oxygen for each ecies and temperature were estimated sub- tively by inspection of the figures and represented by the vertical lines drawn reon. These lines could be placed with nsiderable confidence in most cases because re were remarkably sharp breaks in the tributions of points. In all shock tests ne fish were tested at concentrations of solved oxygen which subsequently proved to well above the critical level. Data from y those fish which were tested near the tical level are plotted in Figures 3, 4, and Some tests near the critical level were ntinued beyond 24 hours. The survival of se fish for 48 hours and longer indicated t fish which were able to survive the first 24 hours of a test could continue to live at that oxygen concentration for at least several days. It therefore seemed justifiable to set 24 hours as the standard survival time and to terminate the tests after that time.

Bluegills

The first fish tested at 25° C. were taken from well-aerated water and placed directly in test vessels through which water with low dissolved oxygen was flowing. Under these conditions of treatment the critical dissolved-oxygen level determined from 18 fish averaging 7 grams each in weight was 1.5 p.p.m. These tests were subsequently repeated allowing a 24-hour rest period in the test vessels before the dissolved oxygen in the inflowing water was lowered. Twenty fish averaging 5 grams each and 14 fish averaging 20 grams each were so tested. The critical dissolved-oxygen level for both the 5-gram and 20-gram fish was estimated to be 0.75 p.p.m. Since there was no difference in the results obtained with these two size groups they are combined in Figure 3. A comparison of the critical levels estimated with and without the 24-hour rest period demonstrates clearly the effects of handling upon the fishes' ability to survive the stress of low dissolved oxygen. In all of the tests with bluegills at 30° C. a 24-hour rest period was allowed before the oxygen was lowered. Sixteen fish having an average weight of 6 grams were tested, and the critical oxygen level was estimated to be 1.0 p.p.m. (Figure 3).

Seventeen fish averaging 8 grams in weight were tested at 35° C. without a rest period, and a critical level of 2.0 p.p.m. of dissolved oxygen was estimated. These tests were repeated with 16 fish averaging 10 grams in weight allowing the fish a 24-hour rest period in the test vessels. The estimated critical oxygen level under these conditions was 1.23 p.p.m. The experiments at 35° C. therefore confirm our observations at 25° C. regarding the importance of allowing test fish time to recover from the effects of handling before subjecting them to additional stress.

Largemouth bass

All of the largemouth bass tested were allowed a 24-hour rest period in the test vessels before they were subjected to low dissolved oxygen. The critical levels of dissolved oxygen at 25° C., 30° C., and 35° C. were estimated to be 0.92, 1.19, and 1.40 p.p.m. respectively (Figure 4). Ten fish averaging

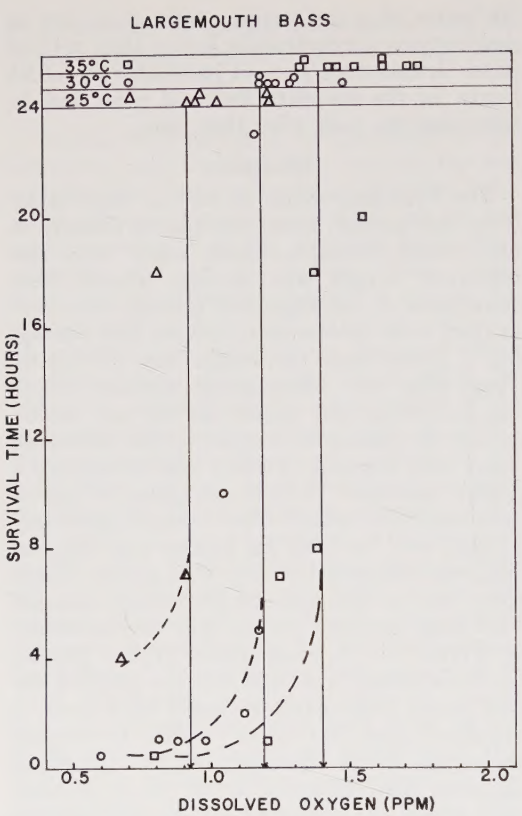


FIGURE 4.—Results of shock tests with largemouth bass showing survival times up to 24 hours at various dissolved-oxygen concentrations at 25° C., 30° C., and 35° C.

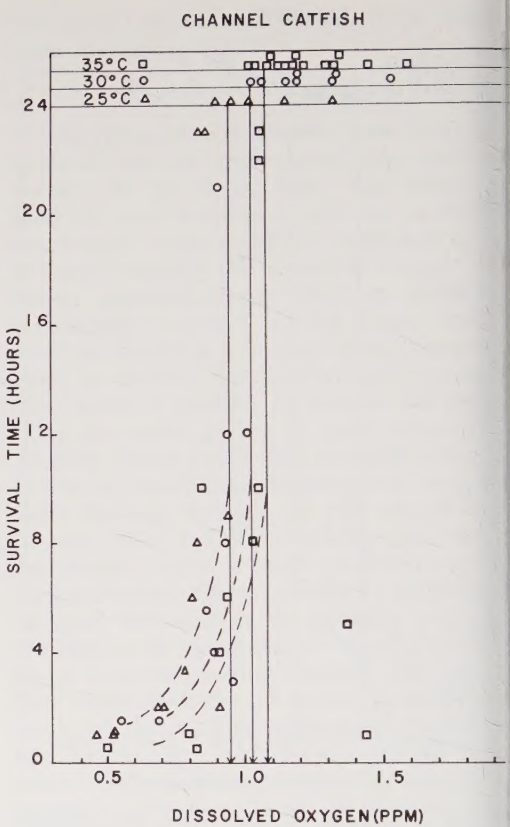


FIGURE 5.—Results of shock tests with "norma channel catfish showing survival times up to hours at various dissolved-oxygen concentrations 25° C., 30° C., and 35° C.

14 grams each were tested at 25° C., and 15 fish averaging 4 grams each were tested at 30° C. Another lot of 15 fish also averaging 4 grams in weight was tested at 35° C.

Channel catfish

All of the channel catfish tested were allowed a rest period of 24 hours in the test vessels before being subjected to low dissolved oxygen. A total of 18 fish with an average weight of 13 grams each was tested at 25° C. At this temperature the critical dissolved-oxygen level was estimated to be 0.95 p.p.m. (Figure 5).

Three lots of fish were tested at 30° C. The first two of these lots (plotted together in Figure 6) yielded results which were inconsistent and quite out of line with our other findings. One of these lots contained 16 fish averaging 16 grams each in weight which had been acclimatized to 30° C. for 90 days before being tested in May 1960; the other lot contained 16 fish averaging 15 grams ar was acclimatized for 45 days before beir tested in July 1960. The reasons for the i consistencies in the results obtained with thes two groups of fish have not been fully co firmed, but it is suspected that their nutr tional state was mainly responsible. All these fish were excessively fat, having bee fed very heavily for several months in a effort to bring them up to a size comparab to other fish being tested. Unfortunately me abolic rates were not determined on these fis but it seems likely that these may have bee abnormally high. A third group of 20 fis averaging 22 grams each was acclimatized f 30 days at 30° C. and tested in October 196 These fish were in good condition but we not exceptionally fat. An estimate of 1.(p.p.m. of dissolved oxygen was obtained wi this group of fish. As can be seen by comparison of Figures 5 and 6, this group

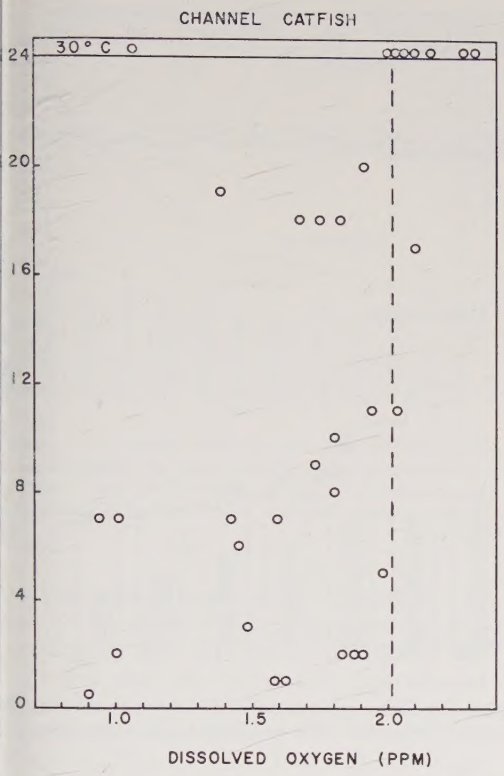


FIGURE 6.—Results of shock tests with "overfed" channel catfish showing survival times up to 24 hours at various oxygen concentrations at 30° C.

sh yielded data which were reasonable and onsistent.

Two groups of fish averaging 18 grams ach were tested at 35° C. Fifteen fish were cclimatized to 35° C. for 45 days and tested n July 1960, and 12 fish were acclimatized 3 days and tested in September 1960. Con-dered separately, these two groups yielded stimates of the critical oxygen level of 1.05 nd 1.09 p.p.m. respectively. These groups re combined in Figure 5 and an estimate of .08 p.p.m. of dissolved oxygen obtained.

RESULTS OF ACCLIMATION TESTS

At least three individuals were tested at ach temperature (25° C., 30° C., and 35° .) for each of the three species. The data n all acclimation experiments in which there as adequate control of temperature and dis-olved oxygen are summarized for the three pecies in Tables 1, 2, and 3. The data on verage oxygen consumption in these tables ere calculated from the individual deter-inations of dissolved-oxygen differences in inflowing and outflowing water. The number of observations used in computing the average consumption are given in the columns headed "*N*," followed by the standard errors of the observations. In all cases the oxygen-consumption values for the first 24 to 48 hours of an experiment were not used since they were invariably higher than normal due to the excitation of the fish. Oxygen-consumption values for the experimental fish for the last 24 to 48 hours of an experiment were also disregarded in calculating the average consumption when these were lower than normal, as in the cases of those fish which exhibited respiratory dependence at low ambient oxygen concentrations. Detailed data from selected typical experiments are presented graphically in Figures 7 through 15.

Bluegills

Four of the five experimental fish tested at 25° C. yielded critical dissolved-oxygen values which approximated each other very closely (0.73, 0.77, 0.77, and 0.78 p.p.m.). These were also very close to the results obtained at 30° C. In the April 1958 experiment at 25° C., however, the test fish did not die until the ambient oxygen dropped to nearly 0.5 p.p.m. The environmental variates in this experiment were better controlled than they were in the others at the same temperature, and it is thus felt that the critical concentration achieved here approximates more closely the ultimate low dissolved oxygen tolerable at this temperature. The results of this experiment are presented graphically in Figure 7. The rates of oxygen consumption at 25° C. are roughly in inverse proportion to the size of the fish tested, but they are not different from the consumption rates of fish of comparable size at 30° C. (Table 1). Detailed data from the control and the 9.3-gram experimental fish tested at 30° C. are presented in Figure 8. Only two of the critical levels determined at 35° C. can be considered valid (those for the 10.3- and 16.5-gram fish). The 33.6-gram fish in the August 1960 experiment was accidentally subjected to a sharp drop (from 3.25 to 1.00 p.p.m.) in ambient oxygen in only 48 hours. This rapid drop in dissolved oxygen doubtless brought about the untimely death of this fish; however, data on its respiratory rate prior to that are valid. Results of the July 26–August 6 experiment are shown in Figure 9. In summary it can be said that our best estimates of critical dissolved-oxygen levels with full opportunity for acclimation

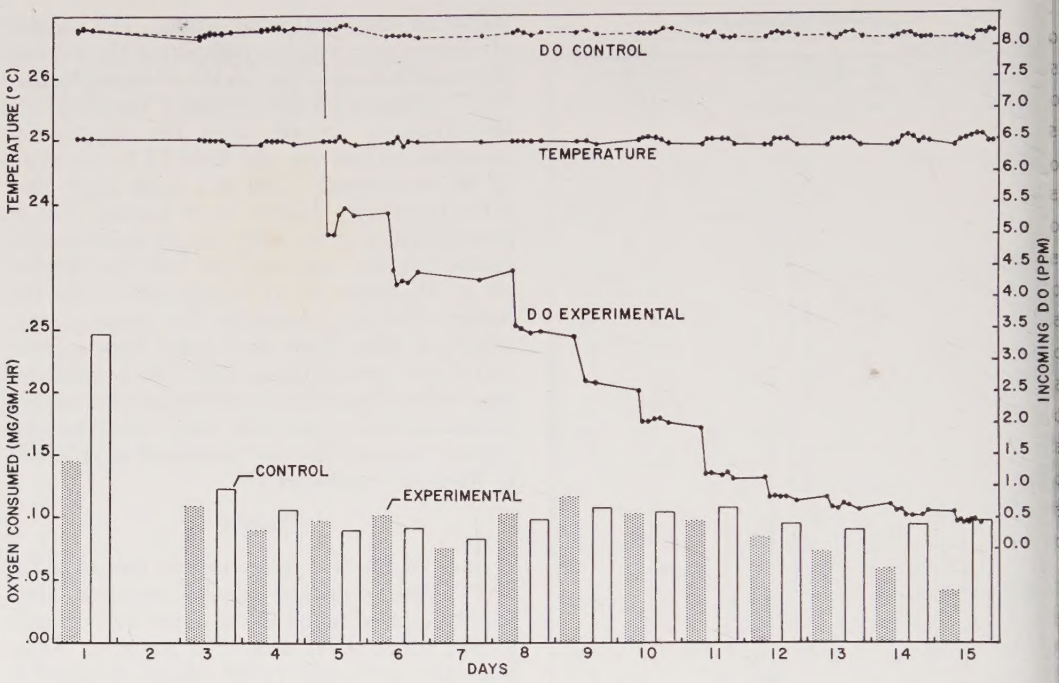


FIGURE 7.—Average daily oxygen consumption and oxygen available to control and experimental bluegill tested April 5–19, 1958. Weights of control and experimental fish were 12.1 and 12.8 grams respectively.

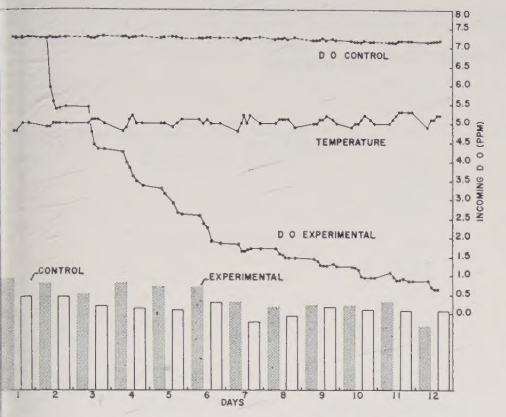
are slightly above 0.5 p.p.m. at 25° C., near 0.8 p.p.m. at 30° C., and slightly above 0.9 p.p.m. at 35° C. These levels apply to fish of about 10 grams weight.

Largemouth bass

The largemouth bass tested at 25° C., 30° C., and 35° C. were unfortunately in three different size groups so that few precise comparisons can be made between the fish at different temperatures. The effect of size on oxygen consumption is evident and reasonably consistent at all three temperatures. It might be expected that this effect would be reflected in differences in the critical dissolved-oxygen levels, but such was not the

TABLE 1.—*Data from acclimation experiments with bluegills*

Temperature (° C.)	Date	Weight (grams)	Critical dissolved oxygen (p.p.m.)	Average oxygen consumed (mg/gm/hr)	*N*	Standard error
25	March 13–26, 1958	7.3	Control	0.123	63	0.003
		9.1	0.73	0.125	57	0.003
	April 5–19, 1958	12.1	Control	0.100	70	0.002
		12.8	0.51	0.096	57	0.002
	Dec. 4–17, 1959	45.1	Control	0.053	64	0.001
		30.8	0.77	0.061	50	0.003
		48.4	0.77	0.054	58	0.001
		11.9	0.78	0.103	51	0.004
30	June 13–25, 1960	10.4	Control	0.106	65	0.002
		9.8	0.80	0.119	64	0.002
		15.6	0.80	0.096	64	0.002
		9.3	0.77	0.123	60	0.002
35	July 26– Aug. 6, 1958	6.7	Control	0.158	55	0.003
		10.3	0.98	0.148	51	0.002
	Aug. 17–30, 1960	7.1	Control	0.195	57	0.007
		33.6	1.22	0.137	53	0.003
		16.5	0.87	0.170	75	0.004



IGURE 8.—Average daily oxygen consumption and gen available to control and experimental blue- tested June 13–25, 1960. Weights of control and rimental fish were 10.4 and 9.3 grams respec- y.

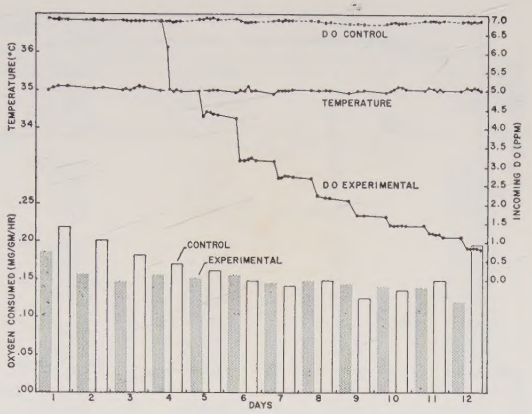


FIGURE 9.—Average daily oxygen consumption and oxygen available to control and experimental bluegills tested July 26–August 6, 1958. Weights of control and experimental fish were 6.7 and 10.3 grams respectively.

. The critical levels at 25° C. and 30° C. ear to be quite similar regardless of size respiratory rate (Table 2). Data for the trol fish and the 23.9-gram experimental ed at 25° C. and for the control and 22.6- m experimental tested at 30° C. are given Figures 10 and 11. The critical levels ained for the five fish tested at 35° C. roximated each other very closely (1.32, 1, 1.20, 1.20, and 1.20 p.p.m.). The fish ed at 35° C. were appreciably larger than se tested at lower temperatures. One con- uence of this fact was that it was not pos- e to maintain as small a drop in oxygen water passing through the test vessels. n when the flow was set at the upper it of the capacity of the apparatus, the gen drop was in the vicinity of 0.5 p.p.m. for the larger fish as opposed to a drop of 0.2 or 0.3 p.p.m. in the cases of the smaller fish. It is therefore probable that the critical oxygen levels obtained with the large fish at 35° C. are slightly higher than would have been the case if these fish had not been required to remove such a high percentage of the oxygen available to them. Results of the 72.0-gram control and the 71.2-gram experimental fish tested at 35° C. August 27 to September 7, 1959, are presented in Figure 12.

Channel catfish

The critical dissolved-oxygen levels determined for channel catfish (Table 3) show little if any relationship to the respiratory rates of the fish, nor is there any clearcut relationship evident between the respiratory rates

LE 2.—*Data from acclimation experiments with largemouth bass*

perature ° C.)	Date	Weight (grams)	Critical dissolved oxygen (p.p.m.)	Average oxygen consumed (mg/gm/hr)	*N*	Standard error
25	Dec. 20, 1959–Jan. 7, 1960	12.1	Control	0.100	88	0.002
		4.7	0.78	0.156	53	0.005
		7.8	0.87	0.129	68	0.004
		23.9	0.84	0.089	61	0.002
30	May 30–June 12, 1960	12.2	Control	0.101	72	0.002
		14.7	0.84	0.116	74	0.005
		22.6	0.87	0.109	65	0.002
		14.8	0.79	0.129	57	0.003
35	Aug. 15–25, 1959	97.6	Control	0.114	24	0.003
		62.7	1.32	0.135	52	0.003
		96.0	1.24	0.112	50	0.002
		63.3	1.20	0.150	45	0.003
	Aug. 27–Sept. 7, 1959	72.0	Control	0.119	60	0.002
		71.2	1.20	0.124	53	0.002
		73.5	1.20	0.126	51	0.002

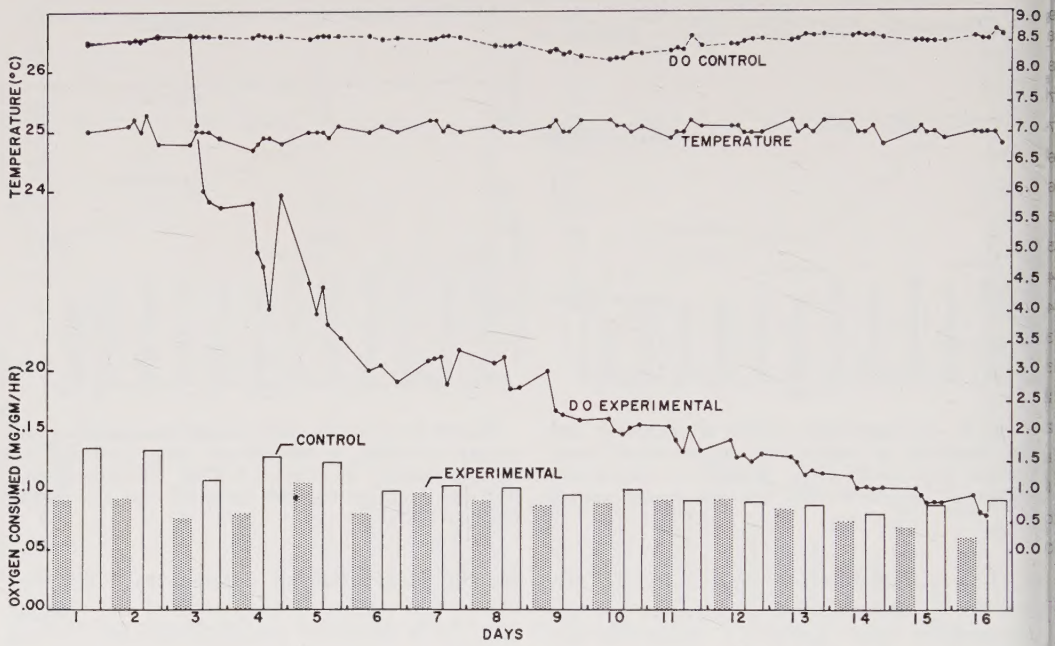


FIGURE 10.—Average daily oxygen consumption and oxygen available to control and experimental larg mouth bass tested December 20–January 7, 1960. Weights of control and experimental fish were 12.1 a 23.9 grams respectively.

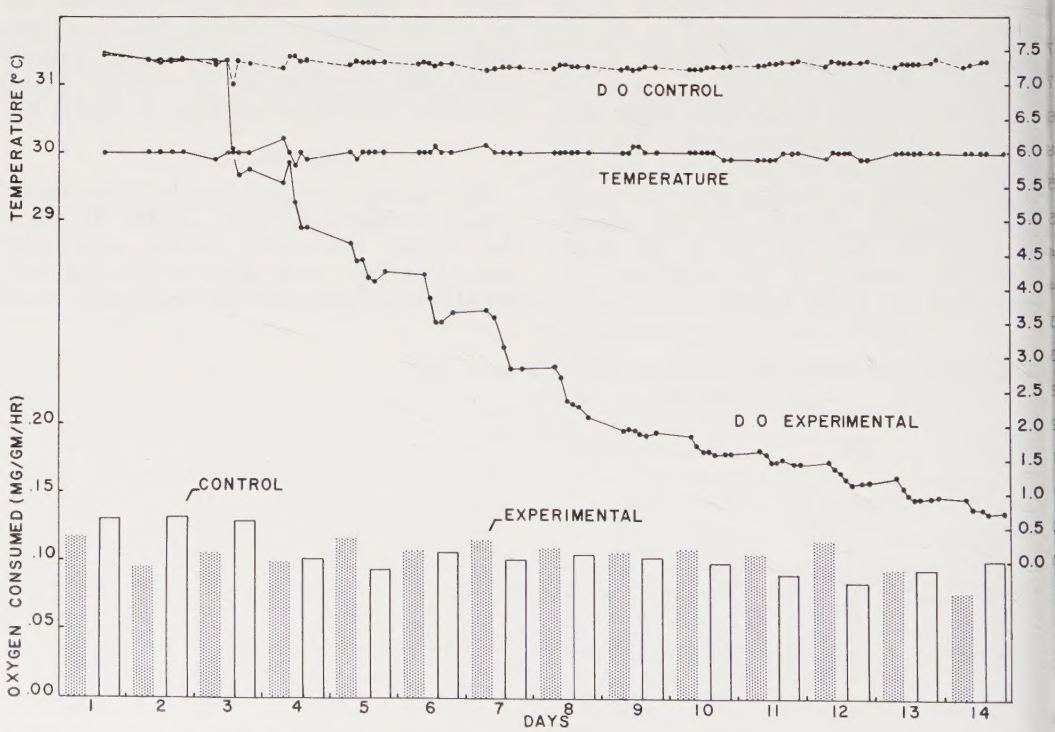


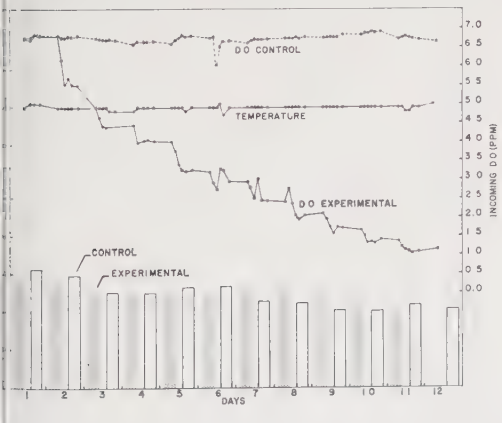
FIGURE 11.—Average daily oxygen consumption and oxygen available to control and experimental larg mouth bass tested May 30–June 12, 1960. Weights of control and experimental fish were 12.2 and 22 grams respectively.

BLE 3.—*Data from acclimation experiments with channel catfish*

nperature (° C.)	Date	Weight (grams)	Critical dissolved oxygen (p.p.m.)	Average oxygen consumed (mg/gm/hr)	*N*	Standard error
25	May 20–31, 1959	74.0	Control	0.120	51	0.003
		75.0	0.82	0.100	37	0.003
		103.3	0.88	0.077	38	0.002
		102.7	0.97	0.092	37	0.002
	June 12–25, 1959	54.4	Control	0.088	63	0.002
		66.6	0.82	0.098	50	0.005
		35.3	0.76	0.106	65	0.005
		59.0	0.72	0.108	42	0.005
	April 2– 16, 1960	24.4	Control	0.083	76	0.002
		21.7	0.78	0.087	75	0.002
		21.7	0.75	0.087	75	0.003
		20.7	0.70	0.093	67	0.003
30	May 9–23, 1960	25.5	Control	0.136	75	0.003
		25.5	0.96	0.129	71	0.002
		32.5	0.85	0.133	60	0.003
		33.7	0.85	0.120	74	0.003
35	July 27–Aug. 8, 1959	57.5	Control	0.171	62	0.011
		68.7	1.06	0.131	66	0.003
	July 31–Aug. 15,1959	57.0	Control	0.121	72	0.005
		60.0	0.83	0.127	66	0.003
	Aug. 29–Sept. 11, 1960	22.6	Control	0.126	70	0.004
		12.5	0.88	0.193	73	0.004
		21.3	0.90	0.137	60	0.004
		33.3	1.12	0.150	64	0.003

d weights of the fish tested at any given nperature. There is evidence, however, that tical dissolved-oxygen levels increase with reasing temperature. Respiratory rates are gher at 30° C. than at 25° C., but at 35° C. y are within the range of rates determined 30° C. (in five out of eight individuals ted).

Two of the nine experimental fish tested at ° C. weighed over 100 grams. These larger h were forced to extract a greater percentage of the oxygen available in the incoming water than were the seven smaller fish. Probably as a result of this additional stress the large fish yielded critical oxygen values slightly higher than the smaller fish. The average critical level for the seven smaller fish was 0.76 p.p.m. of dissolved oxygen. Detailed data from the control and the 21.7-gram experimental fish are presented in Figure 13. The average critical oxygen level for the three fish tested at 30° C. was 0.89 p.p.m., while the average for the five fish tested at 35° C. was 0.96 p.p.m. Data from the control and the 25.5-gram experimental fish tested at 30° C. are presented in Figure 14, and data from the control and 21.3-gram experimental fish tested at 35° C. are presented in Figure 15. The control fish tested at 35° C. July 27 through August 8, 1959, exhibited an anomalous and unexplained respiratory pattern. Its respiratory rate increased steadily for the first 4 days of the experiment and then dropped progressively to a subnormal rate before the end of the experiment. Data from this fish have therefore been excluded from the discussion of respiratory rates. The respiratory rate of the 33.3-gram experimental fish tested at 35° C. August 29 through September 11, 1960, appears to be rather high, but in this case it was consistently so.



IGURE 12. — Average daily oxygen consumption l oxygen available to control and experimental gemouth bass tested August 27–September 7, 1959. ights of control and experimental fish were 72.0 d 71.2 grams respectively.

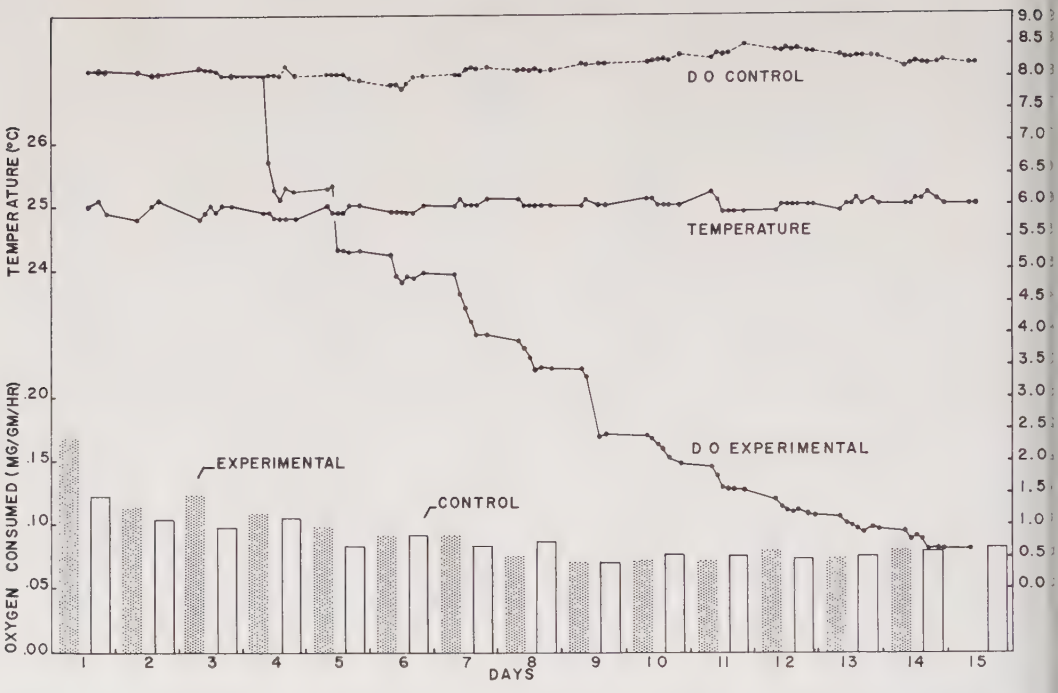


FIGURE 13.—Average daily oxygen consumption and oxygen available to control and experimental cha nel catfish tested April 2–16, 1960. Weights of control and experimental fish were 24.4 and 21.7 grar respectively.

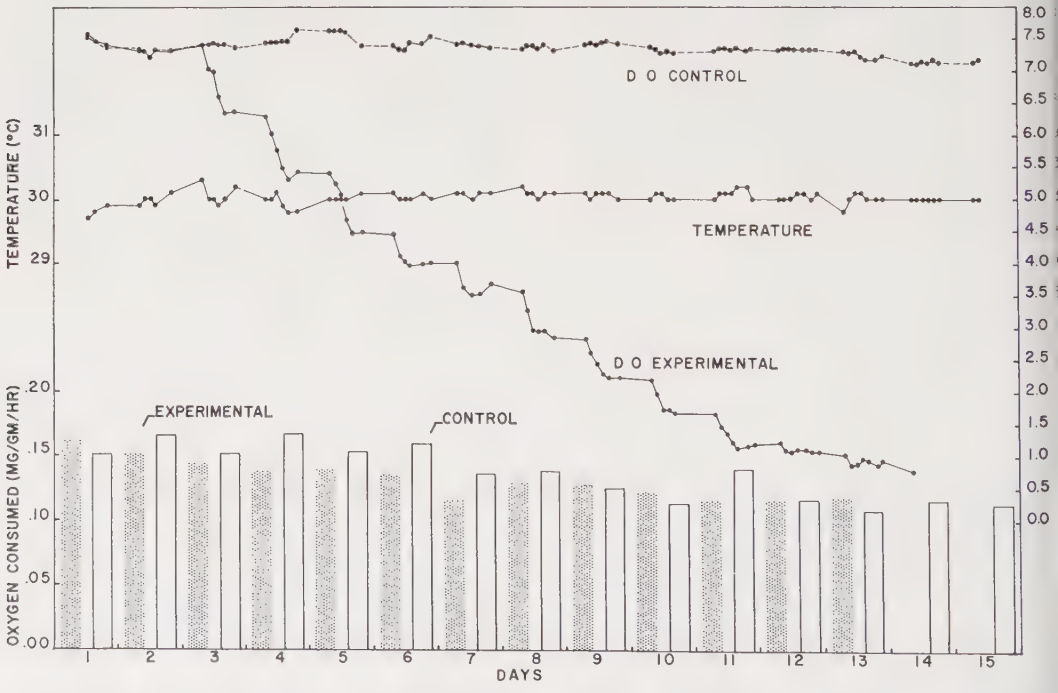


FIGURE 14.—Average daily oxygen consumption and oxygen available to control and experimental chann catfish tested May 9–23, 1960. Weights of control and experimental fish were 25.5 grams each.

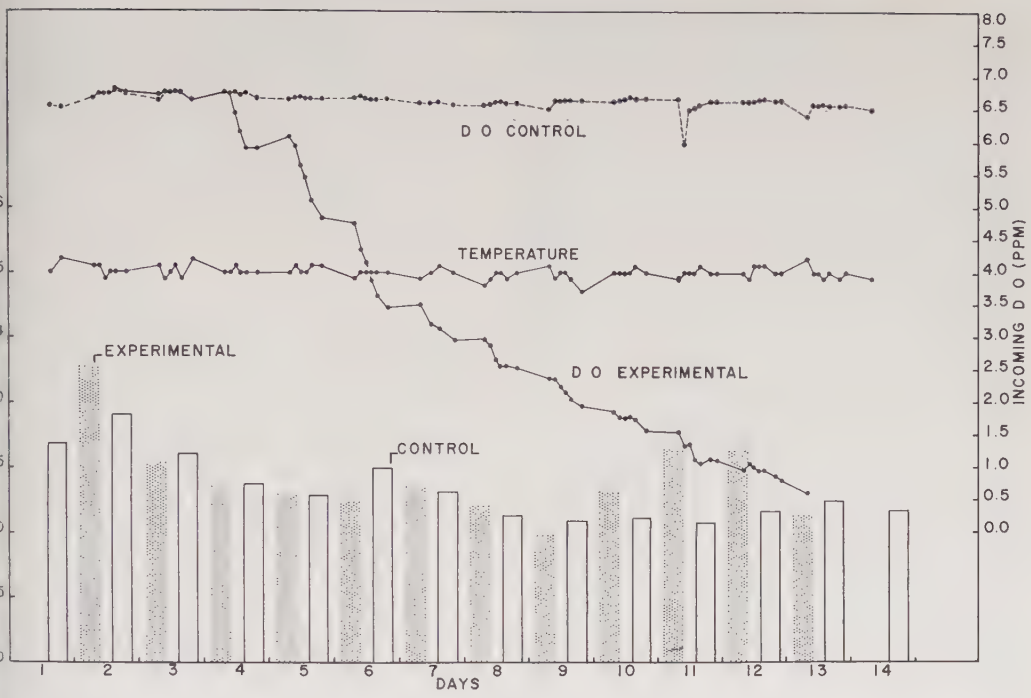


FIGURE 15.—Average daily oxygen consumption and oxygen available to control and experimental channel fish tested August 29–September 11, 1960. Weights of control and experimental fish were 22.6 and 21.3 grams respectively.

DISCUSSION

The ability of an organism to survive low levels of ambient oxygen may be determined by 1) the efficiency of its respiratory apparatus, 2) the efficiency of its pick-up and transport system, and 3) its requirements for oxygen. In theory, any or all of these may be altered in one way or another by various environmental factors. When any of these change to the advantage of the organism, we encounter the phenomenon known as acclimation or adaptation. In the present study no attempt was made to investigate the mechanism of acclimation to low dissolved oxygen, but some information was gathered on the influence of various factors on metabolic rates.

Effect of handling on metabolic rate

A number of investigators have demonstrated that fish consume oxygen at near maximal rates for varying periods of time after having been handled (Winterstein, 1908; Keys, 1930; Wiebe and Fuller, 1933; Wells, 1932, 1935a, 1935b). The act of transferring a fish from one vessel to another invariably results in some degree of excitement and vigorous activity on the part of the fish and the investigator, depending upon the species and the circumstances under which the transfer is made. In its new surroundings the fish may exhibit restless activity for some period of time before becoming quiescent, again depending upon the species and circumstances. It is self-evident that in experimental studies involving the standard metabolism of fish, sufficient time must be allowed between handling and experimental treatment to permit the fish to return to some predetermined metabolic level. Our observations on the metabolic rates of fish used in acclimation tests indicate that for all three of the species investigated, and under the circumstances prevailing in our experiments, an undisturbed period of at least 24 hours in the test vessels was required before metabolic rates returned to stable, standard levels. After this settling-down period relatively consistent and uniform levels of metabolism were maintained by virtually all of the 56 fish involved in acclimation tests. The histograms in Figures 7 through 15 illustrate this phenomenon well.

The first shock tests with bluegills at 25°

C. and 35° C. were invalidated by our failure to recognize the need for a rest period after handling. When bluegills were removed from well-aerated water and placed directly in vessels through which water with critically low dissolved oxygen was flowing, 1.50 p.p.m. and 2.00 p.p.m. of dissolved oxygen were required for 24-hour survival at 25° C. and 35° C. respectively. However, when these tests were repeated allowing a 24-hour rest period before the introduction of oxygen-deficient water, the values required for 24-hour survival were 0.75 p.p.m. and 1.22 p.p.m. respectively.

Effect of temperature on metabolic rate

In most instances where the relationship between metabolic rate and temperature has been demonstrated to approximate the Van't Hoff Law, the organisms have been taken from one temperature (to which they may or may not have been acclimatized) and placed at another temperature, and the metabolic rates obtained at both temperatures compared. Wiebe and Fuller (1933) undoubtedly used this technique when they found a Q_{10} of about 2.8 for the largemouth bass between 15° C. and 25° C. On the other hand, Wells (1935a), Fry and Hart (1948), Graham (1949), Job (1955), and others have demonstrated that when fish have been thoroughly acclimated at various temperatures, metabolic rates do not increase as much as twofold with each 10° C. increase in temperature and that increases become progressively smaller as the upper lethal temperature of the organism is approached (Fry, 1957).

Among fish of comparable size of the three species herein reported, oxygen consumption differed little between 25° C. and 35° C. For example, small bluegills (7 to 16 grams) exhibited virtually the same metabolic rates at 25° C. and 30° C. and showed but a slight increase between 30° C. and 35° C. (Table 1). Largemouth bass of comparable sizes tested at 25° C. and 30° C. likewise showed no appreciable increase in metabolic rate with increasing temperature (Table 2). Largemouth bass of comparable size were not tested at 35° C. Channel catfish showed little increase in metabolic rate between 25° C. and 30° C. or between 30° C. and 35° C. The respiratory rates of a few fish (the 33.3-gram and 57.5-gram channel catfish at 35° C., the 74.0-gram channel catfish at 25° C., and the 16.5-gram bluegill at 35° C.) were not considered in these comparisons because they exhibited unusually high metabolic rates or were anomalous in some other respect.

The metabolic mechanisms of the species here considered appear to be highly adaptive. If given sufficient opportunity for temperature acclimation they tend to operate at the same rate regardless of temperature, at least over the range of temperature here covered.

Effect of size on metabolic rate

It is common practice to express the relationship between size and metabolic rate on a log weight–log oxygen consumption plot. The results usually approximate a straight line with a slope of less than 1.0, indicating that smaller fish have a higher per-gram oxygen requirement than do larger fish (Job, 1955, and others). In studies dealing with tolerance to low dissolved oxygen it is important to make comparisons between fish which have similar relative metabolic rates, in other words, fish of a similar size. In the present work a limited range of sizes was studied in each species, and it was necessary to establish to what degree fishes at the extremes of these ranges were comparable. In all three species the widest range of sizes for which data were available was in the acclimation experiments at 25° C. Relative metabolic rates are plotted against weight for the three species in Figure 16. In both the bluegills and largemouth bass the relative metabolic rate decreases with increasing size up to weights between 10 and 15 grams; beyond this point there is no measurable drop in metabolic rate over the size range tested. No channel catfish were tested that weighed less than 20 grams, but in the range between 20 and 105 grams there was no detectable difference in relative metabolic rate. From these data it may be concluded that intraspecific comparisons can be made in these three species over the size ranges indicated.

Effect of nutritional state on metabolic rate

Smith (1935) and others have reported that starvation in fish is accompanied by a marked and progressive decline in the standard metabolic rate. This appears to be the case when the absolute (whole fish) rate of oxygen consumption is considered, but, when these data are converted to relative rates which take into account the loss of weight by the starved organism, the metabolic rate stabilizes in a few days and remains relatively constant thereafter. Wells (1935a), for example, found that starvation for 7 days ha

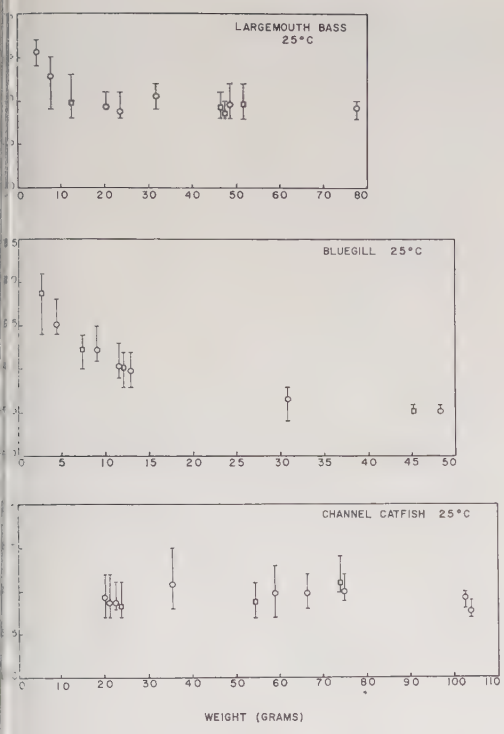


FIGURE 16.—The relationship of relative rates of ndard metabolism to weight in the bluegill, large- uth bass, and channel catfish at 25° C. Circles d squares represent the mean values for individual perimental and control fish respectively. The ver- al lines indicate the extremes of daily average tes of oxygen consumption.

effect on the relative rate of oxygen uptake the California killifish, *Fundulus parvi- nnis*. In the present study no significant ecline was noted in the relative metabolic tes of the control fish used in the acclima- on tests. The rate of oxygen consumption of ese fish was observed over periods of 11 15 days, during which time (and for at ast 2 days prior) they received no food. As inted out elsewhere, the high rates of metab- ism observed in the first 24 to 48 hours of ost experiments were attributable to the fects of handling (see histograms in Figures through 15).

The relationship between obesity and meta- olic rate does not seem to have been investi- ated in fishes. Data from two groups of annel catfish used in shock tests at 30° C. ggest strongly that excessively fat fish are ore sensitive to low levels of dissolved oxy- en than are fish which have been normally d (Figure 6). Unfortunately, oxygen-con- mption data were not obtained on these fish, and until further work can be done on this point, it is assumed that their oxygen requirements were unusually high.

Endogenous metabolic rhythms

Endogenous cycles in standard metabolic rate have been reported for a number of species of fish. These reports have not always been consistent. Clausen (1933, 1936), working with several species of fresh-water fishes, found what he considered to be daily patterns in some species but not in all that he investigated. He stated that the largemouth bass exhibited a definite daily rhythm in metabolic rate which coincided quite closely with the known activity pattern of this species. According to Higginbotham (1947) the channel catfish showed distinctly higher rates of oxygen uptake in the afternoon than in the morning. Spencer (1939) failed to find evidence of a daily rhythm in the rate of oxygen consumption in the bluegill. Graham (1949) noted that the standard metabolism of the brook trout, *Salvelinus fontinalis*, exhibited a daily fluctuation with the low point occurring between midnight and early morning, but Job (1955), working with the same species, found that in only 60 percent of his experiments did the minimal oxygen consumption occur at this time of day.

The acclimation experiments herein reported provided daily oxygen-consumption data on many individual fish for 14 or more consecutive days at three different temperatures. A careful examination of these data revealed no evidence of consistent diurnal rhythms in oxygen consumption in any of the three species studied. Other experiments were performed with blinded bluegills and channel catfish in which oxygen consumption was measured at closer intervals around the clock. These experiments confirmed the absence of systematic diurnal fluctuations in the standard metabolic rates of these two species. It is possible that daily changes in metabolism did occur which were of such a low order of magnitude (less than 10 percent) that they were not detectable by the methods used, and it is also possible that if the activity of the fish had not been so severely limited by the size of the test vessels they might have shown diurnal activity rhythms which would have been reflected in their metabolic rates. Either or both of these factors might well account for the discrepancies encountered in the literature.

Effect of low dissolved oxygen on metabolic rate

It has been adequately demonstrated that resting fish of most species consume oxygen at rather constant rates over a wide range of ambient oxygen tensions (Hall, 1929; Wiebe and Fuller, 1933; Wells, 1935a, 1935b). At low levels of dissolved oxygen, however, oxygen consumption becomes dependent upon its concentration in the environment. The point at which this shift to oxygen-dependent metabolism occurs (the incipient lethal level) depends upon the degree of activity and thus upon the oxygen requirements of the fish. Shepard (1955, Figure 1) presents these relationships very clearly. Fish entering the oxygen-dependent phase of metabolism are obviously on a downward path that will ultimately lead to death unless activity is reduced or dissolved oxygen increased. The former possibility is not open to resting fish. The incipient lethal level for resting fish is often not reached until the oxygen concentration is lowered to levels that are rapidly fatal. In other words, the zone of resistance of resting fish may be very narrow.

In the acclimation tests of the present investigation, respiratory dependence was encountered in most of the experimental fish that died during that part of the day in which closely spaced observations of metabolic rate were made. Respiratory dependence did not usually set in until 2 to 6 hours before death and was thus seldom observed in those fish that died during the part of the day when no observations were made (12 m. to 8 a.m.). The brevity of the period of respiratory dependence enabled us to use with confidence many of the data on respiratory rates of experimental fish as well as control fish in the foregoing discussion.

Shock and acclimation tests

While the results of the shock and acclimation tests are reasonably consistent within themselves for each species, inter-test and inter-specific comparisons show much less consistency (Table 4). With one exception the critical dissolved-oxygen levels in all tests within each species show a progressive increase with increasing temperatures from 25° C. to 30° C. to 35° C. The one exception is the series of acclimation tests on largemouth bass at 30° C. which yielded results identical with those obtained for this species at 25° C. The critical dissolved-oxygen levels determined in acclimation tests for each speci and at each temperature are invariably low than their counterparts determined in t shock tests, although only in the channel ca fish are these differences consistent. The di ferences between shock and acclimation tes vary from 0.05 p.p.m. in the case of bluegil at 25° C. to 0.36 p.p.m. in the case of larg mouth bass at 30° C. It was expected th acclimation to low dissolved oxygen wou have produced greater and more consiste differences. Shepard (1955) working wi brook trout at 8.5° C. was able by acclim tion to low dissolved oxygen to reduce t tolerance level of large fingerlings by 0.4 p.p.m. of dissolved oxygen, and of small fi gerlings by 0.78 p.p.m. Prosser *et al.* (1957 found that the point where goldfish switche from oxygen-independent to oxygen-depen ent metabolism was shifted from 2.17 p.p.m in fish not acclimatized to low dissolved ox gen to 1.05 p.p.m. in acclimatized fish. The are substantial benefits compared to those r corded here. It is very likely that the est mates of the critical dissolved-oxygen leve made in our acclimation tests were higher an more variable than they should have bee because of the way in which they were mad The experimental fish in the acclimation test were killed by a slowly diminishing oxyge supply, and the average oxygen concentratio over the last 24 hours of life was designate as the critical level. If death occurred, as often did, during the early morning hou when no observations were made, then mo high values than low were included in t estimate. In order to remedy this difficulty would have been necessary to maintain obse vations around the clock for several days nea the termination of each experiment. Anothe factor which doubtless contributed to makin the critical oxygen estimates of the acclim tion experiments high was the fact that these experiments flow rates were controlle

TABLE 4.—*Critical levels of dissolved oxygen (p.p.m as determined in shock and acclimation tests*

Type of test and species	Temperature (degrees centigrade)		
	25	30	35
Shock tests			
Bluegill	0.75	1.00	1.23
Largemouth bass	0.92	1.19	1.40
Channel catfish	0.95	1.03	1.08
Acclimation tests			
Bluegill	0.70	0.80	0.90
Largemouth bass	0.83	0.83	1.23
Channel catfish	0.76	0.89	0.92

that a measurable drop in dissolved oxygen curred across the test vessels and the meta- ic rates of the fish could be measured. In shock tests flow rates were maintained at ximal levels and the dissolved-oxygen drop oss the vessels thereby minimized. Shock ts as performed here are reasonably good asures of ultimate low oxygen levels, while acclimation tests were mainly valuable for data they provided on respiratory rates.

ACKNOWLEDGMENTS

he authors wish to express their thanks to H. S. ngle, Auburn University, and to Jack Snow, Na- al Fish Hatchery, Marion, Alabama, for supply- channel catfish. Harry Gehm of the National ncil for Stream Improvement encouraged us to in the work herein reported and with Russell get of the same organization assured us of sup- t. W. B. Cosgrove, Department of Zoology, Uni- ity of Georgia, provided much advice and many able suggestions on physiological problems.

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Toxicity of Endrin to Some Pacific Northwest Fishes

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ABSTRACT

The toxicity of an endrin formulation to spring chinook and coho salmon, rainbow trout, bluegill, mosquitofish, guppies, and the marine threespine stickleback was determined at 20° C. Coho salmon were the most sensitive, with a 96-hour TL_m of 0.27 parts per billion endrin; sticklebacks were the most tolerant. A volume effect was demonstrated; bluegills died at lower concentrations of endrin in aquaria with the smallest number of fish. Temperature had a marked influence on toxicity of endrin to bluegills, the toxicity increasing with rise of temperature. Tolerance of endrin by marine threespine sticklebacks was about the same in waters of different salinities. Developing eggs and early larvae of the stickleback are more tolerant than fully developed fish.

INTRODUCTION

Among the commonly used insecticides, endrin, a chlorinated hydrocarbon, is most toxic to fish (Henderson, Pickering, and Tarzwell, 1959). Endrin has a wide applicability as an insecticide and is being actively promoted in the agricultural trade literature. The toxicity of endrin to fish is already a matter of concern in Japan, where kills have occurred in fisheries establishments adjacent to rice paddies in which endrin was used (Iyatomi *et al.*, 1958). Formulations of endrin are being used in the Orient to harvest market fish and even are replacing rotenone in areas where derris root is endemic (Kong, 1960). Fishery-management agencies are also searching for compounds that can be applied in population-management procedures (Prevost, 1960). Endrin's great toxicity and its ready availability may make this substance valuable for use in fishery-management practices. Knowledge regarding the toxicity of endrin to fish and of the factors that may influence its effectiveness is desirable.

A study was carried out during late 1958 and early 1959 to determine: the toxicity of endrin to some fish species found in the northwestern United States; the effects of salinity on its toxicity to the euryhaline marine threespine stickleback, *Gasterosteus aculeatus*; the volume effect associated with detoxification of endrin solutions by fishes; the influence of temperature on toxicity of the formulation; and the effects of endrin on the early development and hatching of fertilized stickleback eggs. The study was made in the Pacific Cooperative Water Pollution and Fisheries Research Laboratories at Oregon State Colleg

METHODS AND MATERIALS

Endrin is the trade name for a compou with the chemical formula of 1,2,3,4,10,1 hexachloro-6,7,-epoxy-1,4,4a,5,6,7,8,8a-octah dro-1,4-endo,endo-5,8-dimethanonaphthaler Pertinent chemical and physical data relati to endrin are given by Shell Chemical Corp ration (1954). The formulation used in th study was a powder containing 75 perce endrin, with the remainder consisting of clay absorptive carrier and a stabilizer whi is either urea or hexamethylene tetramine. T stabilizer in the sample tested, if added a cording to Shell Chemical Corporation's re ommendations, should be about 1.25 perce or less by weight of the total formulation. T stock solution used for the making of ser dilutions for testing consisted of 100 mil grams of the dry formulation dispersed 1,000 milliliters of distilled water.

Fish used in the bioassays were rainb trout (*Salmo gairdneri*) of sea-run or ste head strain from the Marion Forks Hatche of the Oregon Fish Commission; spring c nook salmon (*Oncorhynchus tshawytsch* from the McKenzie Salmon Hatchery of t Oregon Fish Commission; wild coho salm (*Oncorhynchus kisutch*) collected from t Yaquina River and the Big Elk River, Linc County; bluegills (*Lepomis macrochirus*) a the mosquitofish (*Gambusia affinis*) tak from ponds near Corvallis; and guppies (*L bistes reticulatus*) from our laboratory sto Marine threespine sticklebacks (*Gasteroste aculeatus*) were collected in the tidal slou areas adjacent to Yaquina Bay, Oregon.

The chinooks varied from 6 to 8 grams

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ABLE 1.—*Toxicity of an endrin formulation at 20° C. to rainbow trout, coho and chinook salmon, guppies, bluegills, and* Gambusia

edian tolerance limits (TL_m) expressed in parts per billion active ingredient]

TL_m	Rainbow trout	Coho salmon	Chinook salmon	Gup-pies	Blue-gills	*Gam-busia*
-hour TL_m	2.17	12.0	—	—	—	—
-hour TL_m	1.45	0.56	1.50	—	—	1.80
-hour TL_m	1.12	0.30	1.01	1.10	0.95	1.05
-hour TL_m	0.90	0.27	0.92	0.90	0.60	0.75

ight. Rainbows averaged 1 gram and were m 1⅝ to 2¼ inches long. Cohos averaged grams and 2½ inches in total length. ppies were from ¾ to 1 inch long. Stickle-cks varied from 1 to 1½ inches in total gth and weighed about 0.3 gram. Bluegills raged 0.45 gram in weight and were from o 1½ inches long.

The guppies were bred in our laboratory d so were acclimated to laboratory condi-ns. Sticklebacks were brought into the oratory and were held in the brackish wa-taken at the site of their capture until use. e other species were stored in outdoor oden tanks supplied with running water m Marys River. These fish were brought o the laboratory and were kept there over-ht before use in a test.

All tests were made in large glass jars which tained 15 liters of Marys River water and propriate amounts of the toxicant. The mbers of fish per test were adjusted so that re was not more than 1.0 gram of fish per r of toxicant solution. Bioassays unless erwise specified were conducted at a con-nt temperature of 20° C. The bioassays re carried out as suggested by Doudoroff *al.* (1951), with the exception that during ts with salmonids the test solutions were ated with compressed air. Aeration was essitated by the high rate of oxygen utiliza-n by these fish.

RESULTS

The 24-, 48-, 72-, and 96-hour TL_m (median erance limits) of the endrin formulation to nbow trout, coho and chinook salmon, ppies, bluegills, and *Gambusia* are listed in ble 1. In Table 2, the 48-, 72-, and 96-hour $_m$ of marine threespine sticklebacks in ckish waters ranging in salinity from 5 to parts per thousand are given. Of the fish ted, the coho is the most sensitive to the drin formulation, with a 96-hour TL_m of 7 p.p.b. (parts per billion) of active in-

TABLE 2.—*Toxicity of an endrin formulation in waters of various salinities at 20° C. to the marine threespine stickleback*

[Median tolerance limits (TL_m) expressed in parts per billion active ingredient]

TL_m	Salinity (parts per thousand)				
	27	25	22	15	5
48-hour TL_m	1.74	2.55	2.40	2.25	2.62
72-hour TL_m	1.71	1.87	1.57	1.71	1.95
96-hour TL_m	1.65	1.50	1.20	1.57	1.57

gredient. Bluegills and *Gambusia* are more tolerant, with a 96-hour TL_m of 0.60 and 0.75 p.p.b. active ingredient, respectively. Rainbow trout, chinook salmon, and guppies are the most tolerant of the species from fresh water, with 96-hour median tolerance limits near 0.9 p.p.b.

The tolerance of marine threespine sticklebacks to endrin is nearly the same in waters of different salinity (Table 2). Variation in the 96-hour TL_m obtained at different salinities may have been due to experimental and sampling errors. The marine stickleback at all concentrations is more tolerant of endrin than the fresh-water species tested, but the data are not sufficient to suggest an antagonistic action of the salt ions.

VOLUME EFFECT

The tolerance of bluegills to the endrin formulation is affected by the number of fish tested in a unit volume of toxicant solution. Prevost, Lanouette, and Grenier (1948) discussed the influence of the volume of toxicant solution on the duration of survival of experimental fish. They found that fish died more rapidly in larger volumes of toxicant solution than in smaller volumes. This finding suggests a partial detoxification or protective action by fish in the smaller water volumes. In the experiment reported here, instead of varying the volume of toxicant solution, the same amount of toxicant was used in each test but the number of fish was varied. A series of tests was performed with 5, 10, and 20 fish

TABLE 3.—*Toxicity of an endrin formulation at 20° C. to various numbers of bluegills in the same volume of water*

[Median tolerance limits (TL_m) expressed in parts per billion active ingredient]

TL_m	5 fish in 15 liters	10 fish in 15 liters	20 fish in 15 liters
72-hour TL_m	0.95	2.25	2.70
96-hour TL_m	0.60	0.86	1.10

in 15 liters of toxicant. The median tolerance limits (Table 3) indicate a "volume effect," with fish dying at lower concentrations in jars with the least number of fish. For example, the 96-hour TL_m for bluegills when five fish were tested in 15 liters of water was 0.60 p.p.b. endrin, but when 20 fish were tested in the same volume, the 96-hour TL_m was 1.1 p.p.b.

TEMPERATURE AND TOXICITY

Iyatomi *et al.* (1958) observed that the toxicity of endrin increased at higher temperatures. In a series of experiments conducted during the early months of 1959, similar results were obtained in the present study. Experiments at temperatures of 10°, 15°, 20°, and 25° C. were conducted in a constant temperature room. Tests at lower temperatures, 1.0°–4.5° C. and 3.5°–8.0° C., were conducted out-of-doors during periods of cold weather. In these experiments the daily maximum and minimum temperatures were recorded. Because there was a scarcity of experimental fish, only six fish were tested at each concentration.

The results (Table 4, Figure 1) indicate a marked increase in toxicity of endrin with increases in temperature. At ambient temperatures between 1.0° and 4.5° C., the estimated 96-hour TL_m was 8.25 p.p.b. active ingredient, whereas at 25° C. the 96-hour TL_m was 0.33 p.p.b., indicating a 25-fold increase in toxicity. There was a consistent decrease in the 96-hour TL_m as the experimental temperature increased.

EFFECTS OF ENDRIN ON EMBRYONIC DEVELOPMENT, HATCHING, AND SURVIVAL OF MARINE THREESPINE STICKLEBACKS

Iyatomi *et al.* (1958) found that the eggs of carp (*Cyprinus carpio*) and the snakehead fish (*Channa argus*) were far more tolerant of endrin than were the later developmental stages of the larvae. An experiment during the present study with the eggs of the marine threespine stickleback indicated that endrin is not as toxic to the developing embryos and newly hatched larvae as it is to the adult. A gravid female stickleback was dissected, the egg mass was removed, and the eggs were fertilized by sperm excised from a mature male stickleback. After an exposure of a few minutes to the sperm, the eggs were washed and the egg mass was broken into small clumps of 22 to 38 eggs. These clumps were placed in dishes containing 200 milliliters of 10 parts per thousand salinity water to which endrin had been added.

The endrin had no apparent effect on the early development of those eggs which had been successfully fertilized. Within 4 days embryonic development had progressed to the stage at which the pigmented eyes are visible through the chorion of the egg. There was no obvious effect of the endrin on development 4 days after fertilization, since only 63 percent of the control embryos had developed to the eyed stage, while 67 percent of the embryos at the highest concentration of endrin were eyed (Table 5). There was no pronounced effect upon time of hatching, which took place 8 to 9 days after fertilization. Although none of the endrin-treated eggs had as high a percentage hatch as did the controls (85 percent

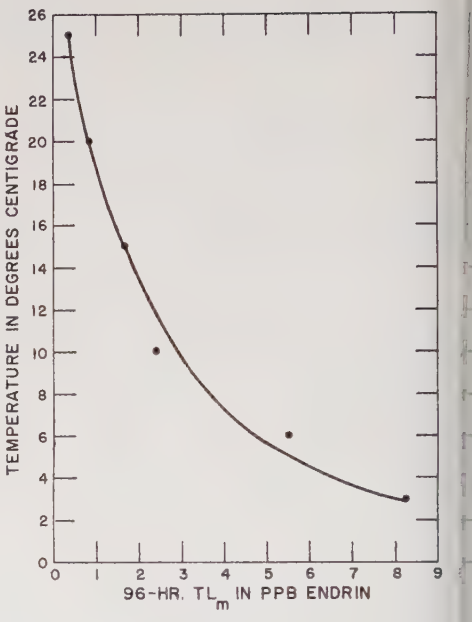

FIGURE 1.—The influence of temperature on the toxicity of an endrin formulation to small bluegills. The 96-hour median tolerance limits (TL_m) are expressed in parts per billion active ingredient.

TABLE 4.—*Toxicity of an endrin formulation to small bluegills at temperatures varying from approximately 3° to 25° C.*

[Median tolerance limits (TL_m) expressed in parts per billion active ingredient]

TL_m	Temperature (degrees C.)					
	3 (1.0–4.5)	6 (3.5–8.0)	10	15	20	25
72-hour TL_m	—	23.2	—	1.95	2.17	0.36
96-hour TL_m	8.25	5.5	2.4	1.65	0.86	0.33

ABLE 5.—*Effects of an endrin formulation on the embryonic development, hatching, and subsequent survival of marine threespine sticklebacks in water of 10 parts per thousand salinity at 20° C.*

P.p.b. active ingredient	Number of eggs	Percentage eyed eggs 4 days after fertilization	Percentage eyed fish hatching in 8–9 days	Number of fish hatched	Percentage survival					
					Days after beginning of hatching					
					3	4	5	6	7	8
Control	38	63	85	20	100	100	85	75	20	5
0.75	32	78	52	13	100	69	61	45	15	0
1.35	21	43	44	4	100	75	75	50	50	0
1.8	27	63	82	13	84	69	61	30	7	7
2.4	22	63	36	5	80	40	20	20	0	0
3.2	24	58	71	10	90	50	10	0	0	0
4.2	36	67	54	13	61	31	0	0	0	0

itch of the eyed eggs), at some concentrations of endrin the hatch was nearly as good as that of the controls (82 percent at 1.8 p.p.b. and 71 percent at 3.2 p.p.b.). Within 4 to 7 days after the fish began to hatch, marked mortalities were observed both in the control and in the endrin solutions. By the fifth day after hatching, a definite pattern of mortality was observed, with great mortalities occurring sooner at the higher concentrations of endrin (Table 5).

The embryos are more tolerant than fully developed fish. It has been shown (Table 2) that the 96-hour TL_m for adult sticklebacks is about 1.2 to 1.65 parts per billion endrin, but over half of the developing eggs hatched at 4.2 p.p.b. after a 9-day exposure. The newly hatched larvae also are more tolerant of endrin than the adult fish, since after 4 days' exposure 50 percent were still alive at 3.2 p.p.b. endrin, which is about twice the 96-hour TL_m for the adult fish.

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Relation Between Water Temperature and Metabolism of Dietary Phosphorus By Fingerling Brook Trout

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ABSTRACT

Fingerling brook trout (*Salvelinus fontinalis*) were force fed a capsulated food that contained P^{32}-labeled phosphorus. A negligible direct effect of water temperature from 36° F. to 66° F. was measured on the recovery of the labeled phosphorus in the tissues of the trout through 4 days after feeding. Warmer water accelerated the rate of passage of the food through the digestive tract and the rate of digestion of the food equally. Consecutive daily feedings at water temperatures of 51°F. and 61°F. produced similar results for both water temperatures.

INTRODUCTION

Unlike calcium, the other major structural mineral of the body, phosphorus is primarily obtained by trout from ingested food rather than from both food and water. The Cortland Laboratory has used radioisotope tracers to study the contribution of food phosphorus to the growth of hatchery trout (Phillips *et al.*, 1959, 1960). Phosphorus conversions (milligrams of dietary phosphorus required for the subsequent recovery of 1 milligram of phosphorus in the fish tissue) ranging from 1.3 to 5.6 were obtained through the influence of several induced environments on brook trout fed synthetic diets. The most efficient conversions were from high-calorie, low-calcium diets fed to fish held in high-calcium water.

Baldwin (1957) gave an excellent review of the literature pertaining to the numerous influences of water temperature on feeding and growth of fish. Many of the influences of water temperature on appetite, digestion, maintenance requirements, and growth affected the utilization of P^{32}-labeled phosphorus by brook trout in the studies at the Cortland Laboratory. The present article is an expanded summary of these temperature effects on the fate of phosphorus from one feeding and from regular feedings of a capsulated synthetic food.

METHODS

Two series of experiments are reported. The first was performed in 1958 and the second in 1959. Fingerling brook trout (*Salvelinus fontinalis*) ranging from 9 to 24 grams live weight were used. The fish were held in aerated aquarium water that was changed daily. For the 1958 experiments, three water temperatures were used (36° F., 51° F., and 66° F.) and for those in 1959, two water temperatures (51° F. and 61° F.). The fish were fed synthetic foods that contained cellu- flour as bulk, with added mineral sources labeled with $H_3P^{32}O_4$. Quantities of the food containing either 0.5 or 2.0 milligrams of labeled phosphorus were weighed into No. 5 gelatin capsules, and the filled capsules were force fed to the trout. The 0.5-milligram phosphorus level represents the normal average daily phosphorus intake of these hatchery fish. A 1:1 calcium to phosphorus ratio was maintained. All diet mixtures contained a red food dye so that the rate of passage through the tract could be observed.

Significance of the results was determined by analysis of variance.

RESULTS

A complete description of the procedures and the original data may be found in previous publications of this laboratory (Phillips *et al.*, 1959, 1960). In these experiments, measurements were made of the effects of water chemistry, temperature, and diet ingredients on the distribution of ingested phosphorus to several tissues of brook trout. In the present paper only the summaries of the effects of water temperature on the phosphorus conversions of the fish are considered (Tables 1 and 2). The first series of experiments (Table 1) was performed on slightly larger fish, but the other experimental conditions were comparable for the 2 years' experiments. Recovery of labeled phosphorus in the fish tissues measured the assimilation and transport of the dietary phosphorus.

Labeled phosphorus from an original feeding

The fish in the first series (1958) received one capsule each of synthetic food. Fish were not fed again before they were killed at either 1, 2, 3, or 4 days after feeding. Upon dissection of these fish, the rate of passage of the

BLE 1.—*Recoveries of P^{32}-labeled dietary phosphorus following an original feeding of capsulated food to fingerling brook trout*

Milligrams of phosphorus per original feeding	Days after feeding	Milligrams of labeled phosphorus per fish			Phosphorus conversion
		Recovered in fish tissues	Recovered in soluble excretions	Total unrecovered[1]	
		Water temperature 36° F.			
0.5	1	0.16	0.01	0.33	3.1
	2	0.21	0.02	0.27	2.4
	3	0.28	0.03	0.19	1.7
	4	0.20	0.05	0.25	2.5
2.0	1	0.43	0.23	1.34	4.7
	2	0.79	0.36	0.85	2.5
	3	0.84	0.43	0.73	2.4
	4	0.85	0.52	0.63	2.4
		Water temperature 51° F.			
0.5	1	0.17	0.10	0.23	2.9
	2	0.19	0.15	0.16	2.6
	3	0.27	0.23	0.00	1.9
	4	0.19	0.26	0.05	2.6
2.0	1	0.47	0.68	0.85	4.3
	2	0.56	0.77	0.67	3.6
	3	0.73	0.78	0.49	2.7
	4	0.62	0.86	0.52	3.2
		Water temperature 66° F.			
0.5	1	0.10	0.07	0.33	5.0
	2	0.20	0.10	0.20	2.5
	3	0.25	0.11	0.14	2.0
	4	0.23	0.12	0.15	2.2
2.0	1	0.73	0.41	0.86	2.7
	2	0.80	0.57	0.63	2.5
	3	0.75	0.60	0.65	2.7
	4	0.71	0.61	0.68	2.8

[1] Represents unassimilated food, feces cleaned from the digestive tract of the fish, and solid feces in the aquarium ter.

od was apparent from the coloration of the d food dye. One day after feeding, the omachs of the fish held in 36° F. water con- ined a softened, red capsule mass; no colora- on was visible in the digestive tract of the sh held in 66° F. water. Four days after the iginal feeding, a red mass was still in the omachs and small intestines of the fish held 36° F. water, while no red coloration was sible in the digestive tracts of the fish held the 51° F. water.

The movement of the bulk of the food rough the digestive tract was retarded by older water temperatures, but the recoveries the labeled phosphorus summarized in able 1 show that the digestion and absorption the mineral nutrients commenced as soon the food mass had softened in the stomach of e fish. Because of the continued presence of e food in the digestive tracts of the fish held colder water, proportionately more of the beled phosphorus was found within their gestive tract tissue. This phosphorus was ansported subsequently to the bony and uscular tissues.

The effect of water temperature on the metabolic rate had a negligible direct influence on the total tissue recovery of the dietary phosphorus from one feeding. Only the phosphorus utilization from the 2.0-milligram level was significantly altered by water temperature. More efficient utilization of this high phosphorus food was made by the fish held in the 36° F. water. The phosphorus conversions indicate that in the two warmer waters 2.0 milligrams exceeded the digestive and absorptive capacity of the fish. The retardation of the passage of the food mass in the digestive tracts of the fish in the 36° F. water allowed time for assimilation of more phosphorus.

The loss of labeled phosphorus through excretions of the fish was also retarded in cold water. This retardation did not affect the utilization of the 0.5-milligram phosphorus level. A water temperature of 51° F. accelerated the excretion of both levels of phosphorus. The increase of unrecovered labeled phosphorus between the third and fourth day after feeding (Table 1) probably represents the incor-

poration of assimilated phosphorus into solid feces. This increase did not occur with the high phosphorus diet in the 36° F. water where the digestion of the food phosphorus was still in progress at this time.

Labeled phosphorus from regular daily feeding

The preceding series discounted the effect of regular feeding. A second series (1959) was designed to determine whether four consecutive daily feedings would alter the effects of water temperature that were previously established for one feeding. Daily forced feeding of brook trout held in 36° F. water was impractical because passage of food at this temperature was slow. The fish were sensitive to daily handling at 66° F. Water temperatures of 51° F. and 61° F., therefore, were used to determine the effect of water temperature on the utilization of daily feedings of labeled dietary phosphorus (Table 2).

The regular feeding increased the labeled phosphorus content of the fish tissues in proportion to the number of feedings. This relationship was not strictly linear, since the assimilation of the phosphorus from the first feeding was continuing after the second and third feedings. The labeled phosphorus content of the stomach and intestinal tissues regularly increased through 4 days of the experiment.

The phosphorus conversions establish that even with regular feeding the 2.0-milligram level is not used as efficiently as the 0.5-milligram level. The temperature-induced rapid passage of the food in 61° F. water is counterbalanced by an increased rate of digestion and assimilation of the regular, daily supply of food. Slightly higher (an average of only 2 percent of the four feedings) tissue recoveries of phosphorus from the high-level food were made from fish held in warm water. The conversion, however, of the 2.0-milligram level in warm water remained poorer than that of the 0.5-milligram level. Conversion of this normal level of dietary phosphorus was not significantly influenced by water temperature even when the fish were fed daily.

DISCUSSION

The sensitivity of isotopic tracers allows short-term measurements of utilization, and these tissue recoveries of labeled phosphorus depended on the interactions of the rates of digestion, assimilation, and excretion. These recoveries, which are graphically summarized in Figure 1, measured only the utilization of the labeled phosphorus rather than a net increase of tissue phosphorus. Whether the labeled phosphorus will be used for growth or replacement depends on the general nutrition of the fish for an extended period. For the short period of the present experiments the tissue recoveries represent the use made

TABLE 2.—*Recoveries of P^{32}-labeled dietary phosphorus following consecutive daily feedings of capsulated synthetic food to fingerling brook trout*

Milligrams of phosphorus per daily feeding	Number of consecutive daily feedings	Milligrams of labeled phosphorus per fish[1]			Phosphorus conversion
		Recovered in fish tissues	Recovered in soluble excretions	Total unrecovered[2]	
		Water temperature 51° F.			
0.5	1	0.28	0.05	0.17	2.0
	2	0.52	0.14	0.34	2.2
	3	0.74	0.21	0.55	2.2
	4	1.28	0.26	0.44	1.7
2.0	1	0.73	0.32	0.95	3.0
	2	0.85	0.76	2.39	5.0
	3	1.57	1.23	3.20	4.1
	4	2.34	1.78	3.88	3.6
		Water temperature 61° F.			
0.5	1	0.31	0.03	0.16	1.7
	2	0.54	0.07	0.39	2.0
	3	0.98	0.11	0.41	1.6
	4	1.07	0.17	0.66	2.0
2.0	1	0.67	0.19	1.14	3.3
	2	1.09	0.60	2.31	3.8
	3	1.90	1.02	3.08	3.3
	4	2.48	1.62	3.90	3.4

[1] Measured 24 hours after final feeding.
[2] Represents unassimilated food, feces cleaned from the digestive tract of the fish, and solid feces in the aquarium water.

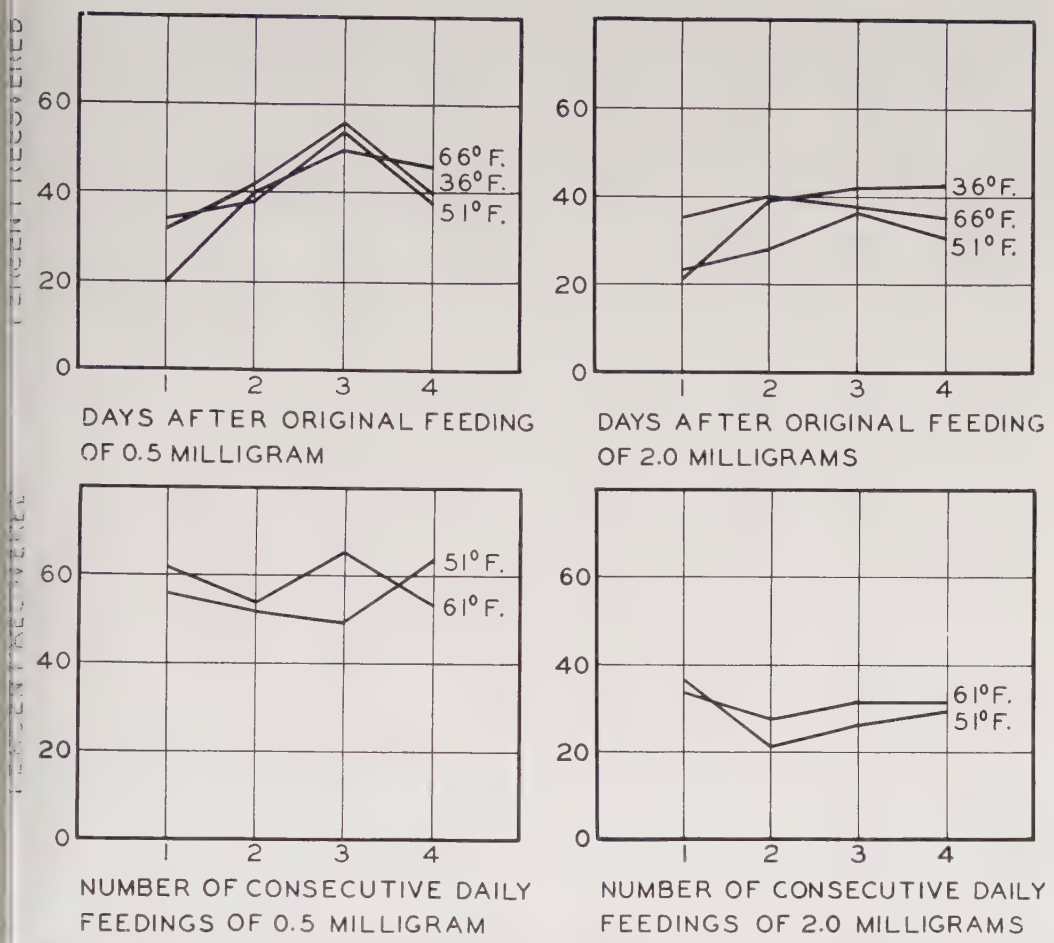

FIGURE 1.—Influence of water temperature on the recoveries of labeled dietary phosphorus (P^{32}) in the tissues of fingerling brook trout after feeding at different rates.

the fish of the phosphorus independently of environmental and biological influences other than water temperature.

Recognizing that utilization of more complex nutrients (protein, for example) might be more sensitive to body temperature, it remains true that the quantity of a nutrient that can be utilized is a function of both the chemical action of the digestive processes and the time of this reaction. Because food passes more slowly at 36° F. and faster at 66° F., neither the decrease nor increase of water temperature from 51° F. significantly affected the phosphorus utilization from one feeding of the normal phosphorus level of the hatchery diet. If all digestible dietary ingredients reacted similarly, the decreased growth rate of trout in cold water is primarily a function of food-mass retention in the stomach. This retention improved the utilization of phosphorus from one feeding of the 2.0-milligram level, but this retention would also act to prevent future feeding of the fish and thus prevent further phosphorus nutrition.

Although the high level supplied four times more phosphorus to the fish, only about two times more of this phosphorus from the four consecutive daily feedings was utilized at either water temperature of the second series of experiments (Figure 1). Proportionately less of the phosphorus fed at the high level was utilized by the trout, while more of this phosphorus appeared in the soluble excretions of the fish (Table 2). Compared to the 0.5-milligram level, this poorer utilization indicates passage of the 2.0-milligram level through the tract with incomplete digestion. The digestion was not improved by warmer

water temperatures since the increase in chemical action (digestion) was counterbalanced by the decrease in reaction time (passage). Because there was an opposite effect of temperature on these two actions, water temperatures which do not cause distress or cause a reduction of appetite have only a minor influence on the utilization of phosphorus by brook trout.

The validity of these experiments depends on the assumption that the food artificially placed in the stomach is acted upon in the same manner as though the fish had fed voluntarily. The same quantity of dietary bulk was forced into the fish at all four temperatures in the two series of experiments. The capsule of food filled from 50 to 100 percent of the stomach capacity. Needham (1930) found that the stomachs of mature brook trout were distended in the summer to 100 percent and in the winter to only 25 to 35 percent of capacity. At water temperatures of 37° F. only 10 percent of their stomach capacity was utilized. According to Needham these values probably reflect the lessened natural food supply in winter, but the appetite of the fish could act to limit the feeding activity in cold water.

Appetite and digestion

At the cold water temperature (36° F.) of the first series of these experiments, portions of the one capsule of food remained in the stomach for 4 days as a deterrent to further feeding. At the water temperatures of the second series of these experiments (51° F. to 61° F.), similar utilization of phosphorus occurred, uninfluenced by water temperature, without the presence of remnants of previous meals in the stomach of the fish. These results lead to the conclusion that because there is mechanical obstruction of the digestive tract, brook trout living in 36° F. water would have to limit either their daily food intake or frequency of feeding by a factor of one-fourth that at 51° F.

Baldwin (1957) measured the consumption of minnows by yearling brook trout and found that the amount eaten approximately doubled for each 4° C. rise in temperature to 13° C. (56° F.). This voluntary feeding corresponds closely to a rate predictable from the present experiments and could be related to the time required for the bulk of the food from one meal to pass out of the stomach. Baldwin found that at 13° C. the trout consumed approximately 50 percent of their body weight in minnows weekly, at 17° C. (63° F.) feeding activity decreased, and at 21° C. (70° F. only 6 percent of their body weight was consumed weekly. The extent of this physiological deterrent to feeding in excessively warm water was very large.

In the warm water (66° F.) of the first series of the present experiments, the fish showed signs of stress which included loss of equilibrium and regurgitation of the capsules. This stress would act as a physiological deterrent to voluntary feeding. Under conditions of forced feeding of one meal, and through elimination of the effects of appetite and digestion rate, brook trout in water temperatures from 36° F. to 66° F. made similar use of dietary phosphorus.

Working with bass, Markus (1932) measured the effect of water temperature on the completeness of their digestion of minnows. None of the bass took food unless the stomach was empty. Small bass fed voluntarily at temperatures from 4° C. (36°F.) to 34° C. (94° F.). Larger bass had to be force fed at temperatures of 10° C. or below. A greater metabolic rate of smaller bass significantly affected their appetites. In the range between 4° C. and 16° C. (64° F.), the digestion rate of 40-gram bass approximately doubled for each 6° C. rise in water temperature. Their digestion rate was increased by a factor of four times as the water temperature increased 6° C. from 16° C. to 22° C. (72° F.).

These irregularities in the digestion rate coupled with the possibilities of stress at both high and low water temperatures, show that while the utilization of nutrients supplied to the fish stomach is relatively independent of water temperature, the metabolism of the fish strongly affects the periodic replenishment of the nutrient supply.

Maintenance and growth

When the trout in the present experiments were force fed one capsule in 36° F. water efficient utilization of phosphorus was measured 4 days later even though a portion of the bulk of the food remained in the stomach. This bulk could be considered a deterrent to further feeding, although the tracer measurements showed that the fish had actively metabolized one of the nutrients. Since the maintenance requirement for any nutrient would be lessened by the lower water temperature (Pentelow, 1939), the phosphorus may satisfy the fish and allow survival with reduced growth. The relative maintenance requirements, food for vital processes and the move

nt activities of the body, were found by ntelow to be independent of the size of wn trout; these requirements more than ubled as the water temperature increased m 50° F. to 59°–66° F.

When the trout of the present experiment re periodically fed identical amounts of sphorus at temperatures (51° F. and 61° that allowed emptying of the stomachs, t did not cause stress, and that should cause ferent relative maintenance requirements, conversion of the dietary phosphorus was atively unaffected by water temperature. ce the maintenance requirements should e risen in the warmer water, the utilization the phosphorus for growth purposes was measured. As summarized by Brown 46) the effect of increasing water temature is to increase both the food eaten by t and their maintenance requirements. e growth rate varies with the ability of the to digest more food than is required for intenance at that particular water temrature.

CONCLUSIONS

n these experiments the recovery of labeled sphorus in fish tissues represents utiliza- n for both maintenance and growth. Weeks controlled feeding of populations of trout uld be required to measure phosphorus owth," with no certainty that extraneous luences on the anabolism of the fish were affecting their phosphorus utilization. er short time periods the tracer label alvs a relatively unconfounded measurement the metabolism of dietary phosphorus. Expolation of these experimental results to brace all dietary essentials is speculative, coupled with the existing knowledge of n metabolism, would lead to the following nclusions on the artificial feeding of hatch- trout:

1. If attention is given to the rate of passe of the particular nutrient through the digestive tract at low water temperatures, good conversions of that nutrient at a slow growth rate are possible. The rate of passage of the mass of food may differ from that of any particular nutrient.

2. Because digestion is rapid at warmer water temperatures, more frequent feeding should promote increased growth. Although the warmer water promotes increased appetite, the increased maintenance requirements of the fish would require more food to be digested to produce good conversions.

3. At still higher water temperatures, a decline in appetite would decrease the efficiency of conversion unless the feeding rate was correspondingly decreased.

4. With a forced feeding schedule where the factors of digestion, appetite, and maintenance are discounted, water temperatures from 36° F. to 66° F. had an insignificant effect on the utilization of dietary phosphorus by fingerling brook trout.

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Recoveries of Tagged, Hatchery-Reared Lake Trout from Lake Superio

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ABSTRACT

Plantings that totaled 13,384 tagged, hatchery-reared lake trout (*Salvelinus namaycush*)—18, 25, 30, or 37 months old—were made at four Lake Superior localities in 1955–57 to: measure possible increases of return from rearing to greater size and age; study the effect of season of planting on the rate of return; compare returns from different types of tags; and follow the movements of hatchery-reared fish. The great advantage of spring over fall planting, demonstrated for fingerling lake trout in earlier experiments, did not hold for fish planted at ages of 18 to 37 months. The improvement of recovery rates with increase of age over the same 18- to 37-month interval appears to be too small to justify the cost of rearing to the higher ages. The recovery rates were closely similar (3.9 to 4.8 percent) for lower-jaw tags and two types of nylon-streamer tags but were much lower than the rate for Petersen tags (12.4 percent). The pins of Petersen tags render the fish highly vulnerable to entanglement in the webbing of gill nets, the principal gear in Lake Superior. Recoveries of Petersen tags also came earlier after planting than did those of other tags. The time between planting and recovery and the distance traveled by the fish were clearly but not closely correlated. Mean distance between points of planting and recovery increased with time out, and average time out increased with the number of miles traveled. More than half of the recoveries of fish that had been at liberty over 2 years were made within 25 miles of the point of release.

INTRODUCTION

From 1951 to 1958 the production of lake trout (*Salvelinus namaycush*) in the commercial fisheries of the United States waters of Lake Superior decreased an average of 265,000 pounds per year. In 1957 the catch had fallen to 1,190,600 pounds. This was the seventh time since 1879, the earliest year of record, that the yield was less than 2 million pounds. In 1958 the production declined still more to 1,059,700 pounds, an all-time low. A take of 3 million pounds per year is considered average for the more recent period of this fishery (Hile, Eschmeyer, and Lunger, 1951). These declines in landings have accompanied the increase in abundance of the parasitic sea lamprey. It appears that the fate of the lake trout in Lake Superior will parallel that in Lakes Huron and Michigan until control of the lamprey is effected.

Prospects for reduction of sea lamprey stocks now appear to be good. After the sea lamprey is brought under control, a program of restocking the upper Great Lakes will have to be carried out. Before this action is taken, it is desirable to gain more knowledge on the best age and season for planting hatchery-reared lake trout to obtain the maximum survival.

The earliest and most extensive experimental studies of returns from hatchery-reared lake trout were based on fingerling and yearling fish (age-groups 0 and I) that had been marked by the removal of fins. The Wisconsin Conservation Department has made extensi plantings of fin-clipped fingerling and yea ling lake trout in Lake Superior. In 1952–5 they fin-clipped 1,191,300 hatchery-rear lake trout, releasing them in both the fall ar spring. Their report at the annual meetir of the Great Lakes Fishery Committee f 1955[1] stated: ". . . spring planting of lal trout appears to be more desirable than fa planting in the Apostle Island Area of Lal Superior," and in 1958 they reported: "Sin 1955, a total of 4,211 recoveries have bee reported; . . . 3,609, or 89.5 percent ha been spring-planted fish. . . ."

The Bureau of Commercial Fisheries start a similar experiment in 1952 and by 1958 ha fin-clipped and planted 888,400 fingerli lake trout in Lake Superior. In their 19 report to the Great Lakes Fishery Committ they stated: ". . . A total of 91 fin-clipp lake trout had been recovered. . . . Of thes 85 had been planted in the spring and on 6 had been stocked in the fall." Reporting this Committee in 1957, they stated: "R turns indicate conclusively that survival the better from spring plantings."

The program of tagging the larger hatche reared lake trout, begun by the Bureau Commercial Fisheries in 1955 (with Paul Eschmeyer as project leader) and continu through 1957, was an extension of this earli

[1] Minutes of all meetings of this Committee (n the Upper Great Lakes Fishery Committee) h been issued in processed form.

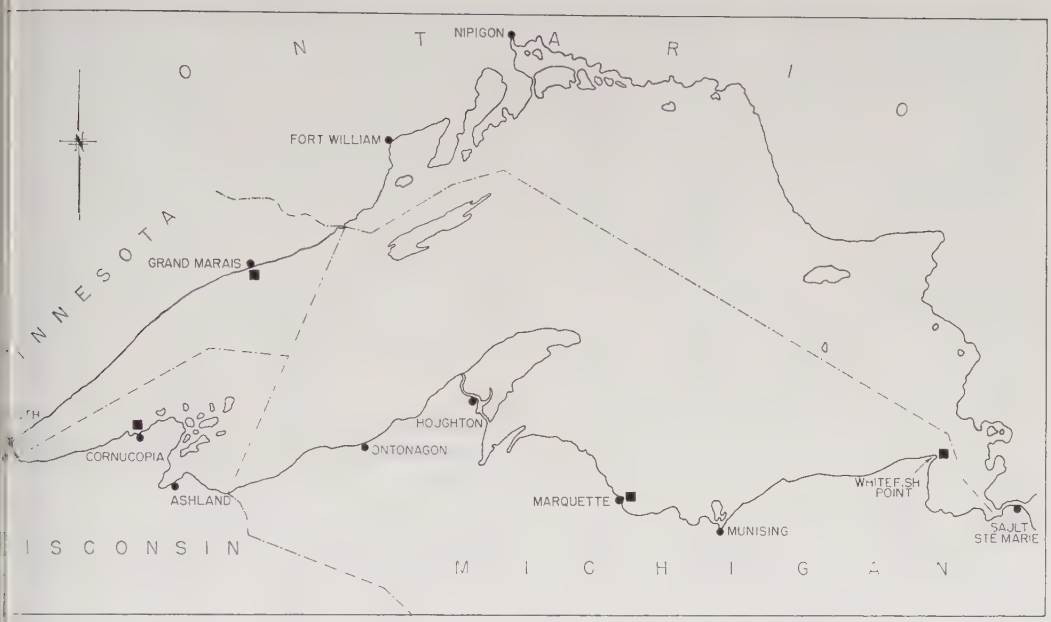

FIGURE 1.—Planting localities (black squares) for tagged, hatchery-reared lake trout released in Lake Superior.

ork. We wished to learn whether the seasonal differences that held for the smaller ke trout extended to fish of larger sizes and eater ages, to gain some knowledge as to ether holding trout in hatcheries a longer riod of time would give greater survival in lake, to determine how fish move after anting at different ages and seasons, and test differences among the several tags with spect to the rate of recapture and growth of e trout. The present report is concerned ith recovery of trout of different ages and ar classes marked with the different tags d planted in different seasons. It deals also ith the relation between time out and dince traveled before recapture.

Reports of recoveries began to fall off arply in the spring of 1959, and the project as terminated on September 30, 1959. The st group of fish planted, therefore, was free pproximately 2 years and 4 months. As few turns could be anticipated after this period, e records can be considered essentially comete for all plantings. The majority of reoveries (74 percent) were reported within e first year, and recaptures after 2 years of eedom were low. The actual time at liberty r the different lots up to the end of the exeriment ranges from 1,452 days (4.0 years) r fish planted in October 1955 to 875 days 2.4 years) for those planted in May 1957.[2]

MATERIALS AND METHODS

The 1954 and 1955 year classes[3] of lake trout were used in this experiment. The 1954 year class came from eggs taken in Lake Superior off Marquette, Michigan, and Munising, Michigan, and the 1955 class from eggs taken in western Lake Superior off the Bad River. The 1954 year class suffered heavy mortality from "blue sac" and " white spot" diseases. These fish were hatched at the Marquette State Fish Hatchery. They were moved to the Lake Mills Federal Station as advanced sac fry and were reared there until April 1955. They were then transferred to the Pendills Creek Fish-Cultural Station located on Whitefish Bay, in eastern Lake Superior. The 1955 year class was hatched at the Lake Mills Federal Station and reared there until the fish were transferred to Pendills Creek in July 1955. These fish suffered only normal mortality. While at Pendills Creek, both lots of fish received the same care and feed and experienced only normal mortality.

Fish hatched in 1954 were tagged and released in October 1955 at an age of 18 months,

[2] Based on midpoint of planting period. For the various sets of releases it took as many as 16 days to plant all of the fish.

[3] The lake trout spawns in the fall, but the eggs hatch the following spring. Year classes are dated by year of hatching.

TABLE 1.—*Number of lake trout tagged and released by tag type, age, year class, and locality of planting*

Date planted and type of tag	Year class and age (months)	Number planted					Length at planting (inches)	
		Grand Marais, Minnesota	Cornucopia, Wisconsin	Marquette, Michigan	Whitefish Point, Michigan	Total	Average	Range
October 1955	1954							
Petersen		137	200	199	200	736	8.4	7.5–10.0
No. 34 streamer	18	178	200	198	200	776	8.4	7.0–10.4
No. 46 streamer		167	198	199	198	762	8.4	7.5–10.2
Lower jaw		183	200	200	200	783	8.4	7.5–10.5
Total		665	798	796	798	3,057	8.4	7.0–10.5
October 1956	1955							
Petersen		198	194	200	196	788	8.5	7.1–10.5
No. 34 streamer	18	99	96	99	96	390	8.4	6.9–10.6
No. 46 streamer		99	97	100	98	394	8.4	7.0–10.3
Lower jaw		200	200	200	200	800	8.4	6.9–11.1
Total		596	587	599	590	2,372	8.4	6.9–11.1
October 1956	1954							
Petersen		100	94	100	100	394	11.9	7.9–14.6
No. 34 streamer	30	50	49	47	49	195	12.0	9.4–14.5
No. 46 streamer		48	50	49	50	197	11.9	8.8–14.6
Lower jaw		99	96	100	100	395	11.9	8.4–15.0
Total		297	289	296	299	1,181	11.9	7.9–15.0
May 1956	1954							
Petersen		197	200	200	200	797	10.0	7.5–12.8
No. 34 streamer	25	201	200	200	197	798	10.1	8.0–12.8
No. 46 streamer		199	201	199	200	799	10.1	8.2–12.5
Lower jaw		200	200	201	200	801	10.0	7.8–12.4
Total		797	801	800	797	3,195	10.0	7.5–12.8
May 1957	1955							
Petersen		198	198	199	200	795	9.8	7.7–14.0
No. 34 streamer	25	99	97	99	100	395	9.9	7.7–12.5
No. 46 streamer		98	98	100	97	393	9.9	7.6–15.4
Lower jaw		200	199	199	200	798	9.8	7.4–12.8
Total		595	592	597	597	2,381	9.8	7.4–15.4
May 1957	1954							
Petersen		100	99	100	100	399	13.7	8.8–17.3
No. 34 streamer	37	49	50	50	50	199	13.7	8.2–17.1
No. 46 streamer		49	50	50	50	199	13.8	8.6–17.2
Lower jaw		101	100	100	100	401	14.0	8.7–17.5
Total		299	299	300	300	1,198	13.8	8.2–17.5
Grand total, average, or range		3,249	3,366	3,388	3,381	13,384	9.8	6.9–17.5

in May 1956 at 25 months, in October 1956 at 30 months, and in May 1957 at 37 months. Fish of the 1955 year class were tagged and released in October 1956 at an age of 18 months, and in May 1957 at 25 months. All tagging took place at Pendills Creek. Fish were anesthetized with tricaine-methanesulfonate.

Portions of each planting were marked with four types of tags (Table 1—see Figure 1 for planting localities): Petersen; streamer tag—No. 34 "Nylock" gill-net twine (tensile strength, 4.5 pounds) with a yellow plastic disc; streamer tag—No. 46 "Nylock" gill-net twine (tensile strength, 6 pounds) also with a disc; and lower jaw. On only two occasions were streamer tags attached by No. 34 and No. 46 thread treated as separate marks (October 1955 and May 1956 releases). On the remaining four the combined lots of streamer tags equalled approximately the numbers marked by Petersen or jaw tags. The Petersen and both types of streamer tags were attached to the fish through the back just posterior to the dorsal fin. These three type of tags carried a serial number and letter; th jaw tag bore a number only. All carried th letters "USFWS" on the reverse side. Eac fish was measured before tagging. The num bers of fish released with each type of ta were similar at the four localities on eac planting date (Table 1), with the exceptio of the October 1955 plant off Grand Marais Minnesota, when high mortality reduced th number stocked.

A form letter was sent to all United State commercial fishermen on Lake Superior ex plaining the project, describing the variou types of tags, and requesting their cooperatio in reporting recoveries. In addition, eac fisherman was sent an addressed post card t facilitate the reporting. The card asked fo information on tag number, date of capture length at capture, location, and depth of wa ter from which the nets were lifted. New pos cards were sent to the fishermen with eac acknowledgment of reports received. As re turns were received, the records were trans

rred to IBM cards. All tables were prepared m IBM tabulations of these records.

No reward was offered for the return of the gs. Most reports were sent directly to the ological Laboratory in Ann Arbor, but some re handled by the Bureau's staffs at Marette, Michigan, and Ashland, Wisconsin. turns were also forwarded to the laboratory A. J. Herridge and J. W. Lockwood, Ontio Department of Lands and Forests; Ben ustafson, Minnesota Department of Conservtion; Russell Daly, Wisconsin Conservation partment; and Leland Anderson, Michigan partment of Conservation.

Leonard S. Joeris, Joseph Beil, Gaylord nderson, and Willis S. Glidden assisted in tagging. The cooperation of the many mmercial fishermen who reported recoveries d of those who assisted in the plantings is eatly appreciated. G. A. Drake, Superinident of the Pendills Creek Fish-Cultural tion, was in charge of the stocking. The ures were drafted by William Cristanelli. lph Hile advised in the analysis of data and the preparation of the manuscript.

RECOVERIES FROM DIFFERENT PLANTING LOCALITIES

Although nearly equal plantings were made f each port, the distribution of recoveries tagged lake trout varied considerably. The mber and percentage of recoveries from ch port was:

Port of planting	Number of recoveries	Percentage of total recoveries
Cornucopia, Wisconsin	309	34
Marquette, Michigan	306	34
Grand Marais, Minnesota	176	19
Whitefish Point, Michigan	117	13
Total	908	—

Circumstances favored a good rate of rn at Cornucopia. Biologists of the Wisconn Conservation Department have had close sociation with Wisconsin fishermen for any years, and in 1957 the Bureau of Comercial Fisheries established a research staon at Ashland. Furthermore, the local fishy has continued to be fairly productive. Wisnsin's annual lake trout catch averaged over million pounds in 1929–56; in 1957 and 58, however, production dropped below 00,000 pounds.

Several factors account for the numerous captures at Marquette. The Marquette–unising area has always been a major contributor to the lake trout production of Michigan waters of Lake Superior (1929–43 average of 18.7 percent). The Bureau has had a field station at Marquette since 1950 and has maintained close contact with the commercial fishermen in the general area. Even though catches from this area have declined, fishing intensity has continued at a substantial level to recent years.

Rapidly declining fishing pressure and the widely scattered fishing operations along the North Shore probably account in part for relatively poor returns from the Grand Marais, Minnesota, plantings. It was reported that some fishermen in this area were annoyed by the use of the Petersen tag because it occasionally became badly tangled in the netting and forced them to cut their twine to release the fish. It is suspected that returns from this area might have been greater if the fishermen had been more willing to cooperate.

Relatively light fishing intensity was surely a factor in the low number of recoveries in the Whitefish Point area. A moderate percentage of the few fishermen in this region do a considerable amount of fishing for whitefish and lake herring. Of the 117 reports from this area, 53 came from Canadian fishermen.

The recoveries from the four planting areas showed similar trends with respect to relative rate of return of the different types of tags and lots of fish, distribution of the recoveries in time, and distance of the movements of fish. For all future consideration, therefore, the data for these localities have been pooled.

RECOVERIES BY TYPE OF TAG

A total of 908 or 6.8 percent of the 13,384 trout tagged were recovered (Table 2). The recovery rate for the 3,909 lake trout released with Petersen tags was 12.4 percent, the highest of any of the four tags used. Recoveries of other types of tags were: 4.5 percent of the 2,753 No. 34 streamer; 3.9 percent of the

TABLE 2.—*Recoveries of lake trout tagged with various types of tags*

[Age groups, planting seasons, and localities combined]

Type of tag	Number tagged	Recoveries	
		Number	Percentage
Petersen	3,909	486	12.4
No. 34 streamer	2,753	125	4.5
No. 46 streamer	2,744	108	3.9
Lower jaw	3,978	189	4.8
All types	13,384	908	6.8
All types except Petersen	9,475	422	4.5

2,744 No. 46 streamer; and 4.8 percent of the 3,978 jaw tags.

The differences among the three "non-Petersen" tags are probably not significant. The numbers recovered were few (125 for the No. 34 streamer, 108 for the No. 46 streamer, and 189 for the lower-jaw tags), and records of returns according to age or season of planting revealed considerable variability in the rate of recovery of each type. Data for these three types of tags were therefore combined.

The advantage of Petersen tags over other types can be judged from the ratio of the percentages of recovery (Table 3). The rate of return of Petersen tags was 2.6 times as great as that of streamer and jaw tags combined for the 1954 year class and 2.7 for the 1955 year class. The advantage of Petersen tags decreased consistently with increase of age at planting.

The recovery rate of the Petersen-type tags was high apparently because this tag becomes easily entangled in the mesh of gill nets. Thus the fish are highly vulnerable to capture as the wire pin tangles in the webbing, regardless of fish size or mesh size. The fish bearing the other three types of tags did not become entangled so easily and hence were taken readily only in nets of appropriate mesh.

RECOVERIES BY AGE GROUP, YEAR CLASS, AND SEASON OF PLANTING

Accurate interpretation of records of recovery by age and year class requires knowledge of the general level of fishing to which each group was exposed following planting. Large annual changes in fishing intensity could place different plantings under widely different pressures and thus influence greatly their expectation of recapture. The only gears that contributed significantly to the capture of tagged lake trout in the present experiment were large-mesh trout gill nets (4½ inches or greater, extension measure) and small-mes chub (deep-water ciscoes—*Coregonus* spp. gill nets 2¼ to 2¾ inches and 3 inches pe mitted in Michigan in water not deeper tha 100 feet). The minimum mesh size for trou nets is 4½ inches in all three states. Th minimum mesh for chub gill nets is 2¼ inche in Minnesota, 2⅜ inches in Wisconsin, an 2½ inches in Michigan.

The relative effectiveness of trout and chu gill nets in capturing the tagged lake trout wa not determined. For fish marked with Pete sen tags, mesh size probably has little bearin on the chance of capture since most fish ar caught by the tangling of the pin in the wel bing of the nets. Lake trout marked with othe types of tags should be taken more readily i chub nets than in trout nets while they ar small. As the fish grow larger they becom less vulnerable to chub nets and more vulne able to trout nets. Legal-sized trout (17 inche or longer) are taken in chub nets and unde sized trout can be numerous in trout nets. Th best estimate of fishing pressure against th tagged lake trout in any single year is prob ably the total amount of gill nets fished fo lake trout and for chubs.

Fishing intensity of trout and chub gill net in the United States waters of Lake Superio (Table 4) was closely similar in 1955 an 1956 and among the 3 years 1957–59, but th difference of level between the two period was considerable. The average total lift fo 1955–56 was 1.34 times that for 1957–5 This shift from a higher to a lower level o exploitation tends to bias returns upward fo fish planted at the younger ages and also t bias the records toward higher returns for th 1954 than for the 1955 year class.

Members of the 1954 year class, planted a 18 months in October 1955 (Table 3) wer subjected 7 months longer to the higher fish ing level of 1955–56 than were fish plante

TABLE 3.—*Percentage recoveries for lake trout marked with Petersen and three other tag types by year clas and age*

Year class and age at planting (months)	Date of planting	Percentage recovered		Ratio of Petersen to others	Average percentage
		Petersen	Others[1]		
1954					
18	October 1955	14.9	3.2	4.7	9.0
25	May 1956	16.2	5.8	2.8	11.0
30	October 1956	17.5	7.5	2.3	12.5
37	May 1957	14.8	7.9	1.9	11.4
Average		15.8[2]	6.1[2]	2.6	11.0[2]
1955					
18	October 1956	6.6	1.8	3.7	4.2
25	May 1957	8.4	3.7	2.3	6.0
Average		7.5[2]	2.8[2]	2.7	5.1[2]

[1] See Table 2.
[2] Unweighted mean.

BLE 4.—*Intensity of the gill-net fisheries for lake rout and chubs in the United States waters of ake Superior, 1955–59*

[Unit is 10,000 linear feet of gill net]

Year	Number of units lifted		
	Lake trout	Chubs	Total
1955	14,729	1,159	15,888
1956	13,747	1,357	15,104
1957	10,143	1,796	11,939
1958	8,397	3,130	11,527
1959	7,395	3,731	11,126

25 months in May 1956, and both of these groups were fished more heavily than the month-old fish planted in October 1956 the 37-month trout planted in May 1957. ke trout of the 1955 year class planted at months in October 1956 probably were ed at a slightly higher rate than the 25-nth-old fish planted in May 1957.

Comparisons of 1954 and 1955 year-class of the same age are limited to lake trout nted at 18 and 25 months. The 18-month- lake trout of the 1954 year class were ex-ited a full year longer at the higher 1955– rate than were members of the 1955 year ss planted at the same age. The 25-month of the 1954 year class planted in May 56 were exploited at the high rate the re-inder of that year whereas all fishing for 55 year-class trout planted in May 1957 s at the lower 1957–59 level.

t is not practical to attempt the correction data to eliminate the effects of the change the level of exploitation, but interpretations comparative records of recoveries of age ups and year classes must be conditioned the knowledge that the change did occur.

The percentage recoveries for the lake trout the 1954 year class marked with Petersen s (Table 3) increased slightly with age m the 18-month-old through the 30-month- fish but fell off for the 37-month-old fish. e percentage recoveries for fish released h the other three tag types increased with from 18-month- through 37-month-old fish. r all types combined, recoveries increased m 18 to 30 months and decreased at 37 nths (but still exceeded the percentage for months). Of the two age groups of the 5 year class planted, the older (25 months) l higher returns than the younger ones (18 nths) for both types of tags. It can be con-ded, therefore, that in general the returns ded to be the greater among fish planted at higher ages. The advantage of the older r the younger fish in percentage of re-capture would have been greater (especially in the 1954 year class) if fishing pressure had been as high in 1957–59 as in 1955–56. Even so, the improvement almost surely would be much too small to justify the cost of building the holding facilities and of rearing the fish to the higher ages—at least within the age range of these experiments.

The rates of recovery from plantings of the 1954 year class far exceeded those of the 1955 year class for fish planted at 18 and 25 months —the only ages at which members of both year classes were stocked (Table 5). The advantage of the 1954 year class as indicated by the ratio of its percentage return to the percentage for the 1955 year class varied with age and type of tag. For both types of tags the advantage of the 1954 year class was greater for fish planted at 18 months than for those planted at 25 months, and for both age groups the advantage of the 1954 year class was greater with Petersen tags than with tags of other types. In general, members of the 1954 year class were returned at a rate about twice that of the 1955 year class. Because of bias from change in the rate of exploitation as previously detailed, we cannot accept the ratio of 2.0 (both age groups, all types of tags) as accurately descriptive of the survival advantage of the 1954 over the 1955 year class. The records of the extent of the change of fishing pressure and of the time each age group was exposed to the higher 1955–56 intensity make it possible, nevertheless, to state with confidence that the survival of the 1954 year class was at least 1.5 times that of the 1955 year class. The cause of the difference between the year classes is not known, but it may be significant that the higher recovery rates were from the year class that suffered heavy mortality in the hatchery. Conceivably this mor-

TABLE 5.—*Comparison of percentage recoveries of tagged lake trout of the 1954 and 1955 year classes*

Year class	Age (months)	Date of planting	Percentage recoveries		
			Petersen	Other	Average
1954	18	October 1955	14.9	3.2	9.0
1955	18	October 1956	6.6	1.8	4.2
Ratio of percentages			2.3	1.8	2.1
1954	25	May 1956	16.2	5.8	11.0
1955	25	May 1957	8.4	3.7	6.0
Ratio of percentages			1.9	1.6	1.8
1954	18, 25	See above	15.6	4.5	10.0
1955	18, 25	See above	7.5	2.8	5.1
Ratio of percentages			2.1	1.6	2.0

tality weeded out the weaker members of this group.

The great advantage of spring over fall plants of fin-clipped fingerlings and yearlings with respect to rate of recapture does not extend to tagged fish planted at greater ages. The interpretation of comparisons of spring and fall plants (Table 3) is complicated by the trend toward increase of recoveries with increase of age at planting and by the change in the level of fishing pressure from 1955–56 to 1957–59. The general conclusion is warranted, however, that any advantage of spring over fall plantings that may exist in older fish is relatively unimportant.

TIME BETWEEN PLANTING AND RECOVERY

Detailed tabulations failed to disclose any trend with age or differences between year classes in the percentage distribution of the total recoveries among the time intervals following planting. Any bias that may have been introduced by the shift in fishing pressure seemingly was obscured by the large differences between the data for different types of tags and seasons of planting. These two factors did influence strongly the percentages of the total number of recoveries obtained in the subsequent periods of time (Table 6, Figure 2). In general, the differences between tags were much greater than the differences between seasons.

A high percentage (69.0 percent) of all recoveries of lake trout bearing Petersen tags and planted in May was returned during the first 3 months. The cumulative percentage of total recaptures had increased to 89.4 percent at the end of 12 months and stood at 97.6 per-

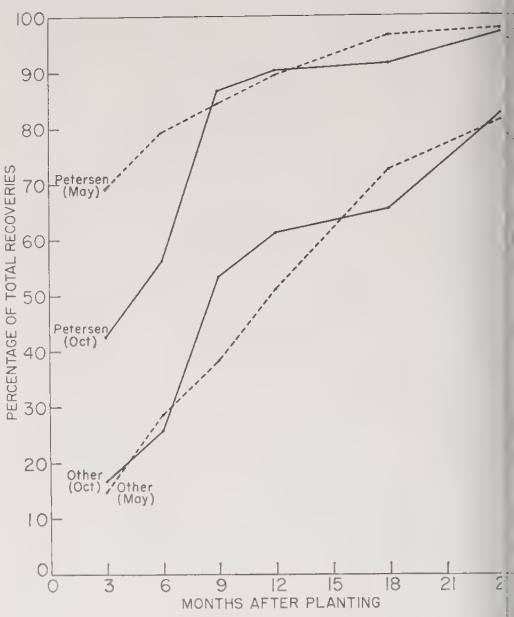

FIGURE 2.—Cumulative percentage of total recove ies of tagged, hatchery-reared lake trout planted Lake Superior according to type of tag and seas of planting.

cent at the end of 24 months. Recapture fish marked with the same tag but planted October proceeded relatively slowly durir the first 6 months (cumulative percentages 42.9 and 56.3 at 3 and 6 months as compare to 69.0 and 79.2 percent for lake trout plante in May). The percentages for the two grou were closely similar, however, at 9 months ar later. Differences between the returns fro May and October plantings during the first months were largely the result of seasonal di

TABLE 6.—*Distribution of recoveries of tagged lake trout through selected time intervals following planti*

[Months are based uniformly on 30 days each]

Tag, month of planting, and item of data	Months after planting							Total recoveri
	<3	3–5	6–8	9–11	12–17	18–23	>23	
Petersen (May)								
Number recovered in period	176	26	13	13	18	3	6	255
Percentage of total recoveries	69.0	10.2	5.1	5.1	7.0	1.2	2.4	—
Cumulative percentage	69.0	79.2	84.3	89.4	96.4	97.6	100.0	—
Petersen (October)								
Number recovered in period	99	31	70	8	3	13	7	231
Percentage of total recoveries	42.9	13.4	30.3	3.5	1.3	5.6	3.0	—
Cumulative percentage	42.9	56.3	86.6	90.1	91.4	97.0	100.0	—
Other types (May)								
Number recovered in period	38	37	25	33	55	23	49	260
Percentage of total recoveries	14.6	14.2	9.6	12.7	21.2	8.9	18.8	—
Cumulative percentage	14.6	28.8	38.4	51.1	72.3	81.2	100.0	—
Other types (October)								
Number recovered in period	27	15	44	13	7	28	28	162
Percentage of total recoveries	16.7	9.2	27.2	8.0	4.3	17.3	17.3	—
Cumulative percentage	16.7	25.9	53.1	61.1	65.4	82.7	100.0	—

rences in fishing pressure. The amount of hing during the 6 months following October ries annually according to weather condi- ns but is far less than the fishing in the 6 nths following May.

Lake trout marked by other tags (streamer d jaw tags) were difficult to capture during e first 6 months after stocking, since fewer an 30 percent of the total recoveries of fish nted in the spring and fall had been made the end of that period. Contrary to the uation with the Petersen tags, the early re- veries of fish planted in May and October re much the same. The cumulative per- tages were much higher for October than May plantings at the end of 9 and 12 nths, but the return for the May stocking s higher at 18 months. The percentages for two groups were nearly the same at the d of 24 months when somewhat more than percent (May, 81.2 percent; October, 82.7 cent) of total recoveries had been made. e temporary separation of the curves at 9 d 12 months can be ascribed to differences fishing pressure exerted against the two ups. During their second 6 months of erty lake trout of the October plantings re in a period of heavy summer fishing. e second 6 months in the lake for May ntings fell in the winter period of limited hing.

In these experiments the early returns came rapidly from fish marked with Petersen s but slowly from those tagged with other es. Most of the recoveries of Petersen tags re within 12 months (about 90 percent of recoveries) and only 3 percent or fewer of e total recoveries were made after 2 years. e streamer and jaw tags were returned in bstantial numbers during the second year liberty, and approximately 18 percent of e total recoveries were made after 2 years.

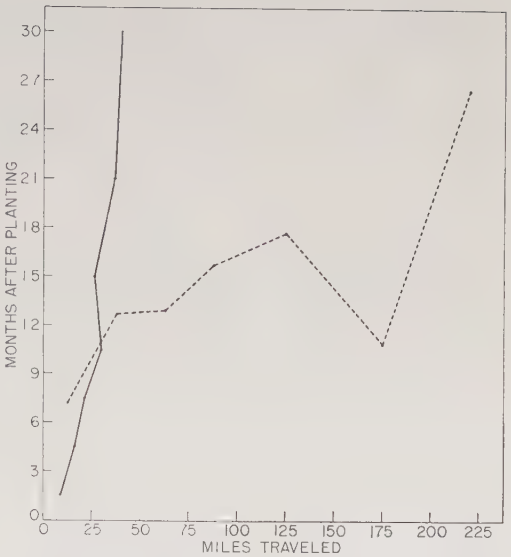

FIGURE 3.—Relation between time out and distance traveled by tagged, hatchery-reared lake trout in Lake Superior. Solid line, mean distance traveled by fish grouped according to time out; broken line, mean time out for fish grouped according to distance traveled.

RELATION BETWEEN TIME OUT AND DISTANCE TRAVELED

Although the timing of the recoveries differed sharply according to type of tag and season of planting, there were no differences in distance traveled other than those attributable to differences in the length of time at liberty. The data for all plantings were combined, therefore, for the preparation of Table 7 and Figure 3.

The period at liberty and the distance between points of planting and recapture were clearly but not closely correlated. None of the 340 lake trout captured within 3 months after planting had moved more than 75 miles

BLE 7.—*Recoveries of tagged lake trout, all types of tags combined, expressed by distance traveled and time out*

Miles traveled	Time out (months)							Total	Percentage	Average time out (months)
	<3	3–5	6–8	9–11	12–17	18–23	>23			
< 26	306	94	105	37	50	35	52	679	74.8	7.2
26– 50	24	8	36	19	23	23	19	152	16.7	12.7
51 - 75	10	3	6	4	3	4	8	38	4.2	12.9
76–100	—	1	3	3	1	1	4	13	1.4	15.7
101–150	—	—	1	3	2	1	2	9	1.0	17.7
151–200	—	2	1	1	2	1	—	7	0.8	11.0
>200	—	1	—	—	1	3	5	10	1.1	26.3
tal	340	109	152	67	82	68	90	908	—	—
centage	37.5	12.0	16.7	7.4	9.0	7.5	9.9	—	—	—
rage distance	9	16	21	30	26	37	40	—	—	—

and most of them (306) were taken within 25 miles. The mean distance for the group was 9 miles. As time out increased, more fish were captured at greater distances but the increase of mean distance was so slow (small decrease at 12–17 months) that the average amounted to only 40 miles for trout at liberty 2 years and more.

Similarly, the increase of average time out for lake trout recovered at successively greater distances was relatively slow and not perfectly regular. The mean period of liberty was shortest (7.2 months) for fish caught within 25 miles of the point of release. It rose steadily with increase of distance to 17.7 months at 101–150 miles but decreased to 11.0 months at 151–200 miles. Ten fish caught over 200 miles from the planting locality, however, had an average time out of more than 2 years, and only one was recaptured in less than 1 year.

The poor correlation between time out and distance traveled resulted from the strong tendency of fish to remain near the point o release regardless of the length of time the had to scatter to other areas. Even among fis that had been free more than 2 years, the ma jority (52 of 90) were recovered within 2 miles of the planting locality. The relatio between time out and movement of thes tagged, hatchery-reared lake trout planted i Lake Superior resembled closely that for sma native lake trout (average length, about 1 inches) tagged in Lake Michigan (Smith an Van Oosten, 1940).

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Hile, Ralph, Paul H. Eschmeyer, and George I Lunger. 1951. Status of the lake trout fishe in Lake Superior. Trans. Am. Fish. Soc., 8(278–312.

Smith, Oliver H., and John Van Oosten. 194(Tagging experiments with lake trout, whitefis and other species of fish from Lake Michiga Trans. Am. Fish. Soc., 69: 63–84.

Selectivity and Efficiency of Experimental Gill Nets in South Bay and Georgian Bay of Lake Huron[1]

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ABSTRACT

Gill-net selectivity curves for ciscoes (*Coregonus artedii*), round whitefish (*Prosopium cylindraceum*), chub species (mainly *Coregonus hoyi*, with a few representatives of *C. reighardi*), yellow perch (*Perca flavescens*), and white suckers (*Catostomus commersoni*) were obtained from the analysis of catch statistics of experimental nylon gill nets fished in Georgian Bay in 1958 and 1959 and in South Bay during the period of 1954 to 1959 inclusive. The method for analysis of the data is similar to that developed by McCombie and Fry (1960). The relative efficiency of nylon and cotton gill nets in catching these species has been compared on the basis of catches of each material made in South Bay. Nylon gill net was found to be 1.3 to 3.6 times as effective as cotton, depending on the species. With the exception of yellow perch, the size composition of catches made with nylon and cotton nets does not differ significantly.

INTRODUCTION

The method developed by McCombie and Fry (1960) for assessing the selectivity of gill nets for the whitefish (*Coregonus clupeaformis*) has been extended in the present study to include the yellow perch (*Perca flavescens*), cisco (*Coregonus artedii*), chub species (mainly *Coregonus hoyi*, with a few representatives of *C. reighardi*), round whitefish (*Prosopium cylindraceum*), and the white sucker (*Catostomus commersoni*). In addition, some comparisons are made between the selectivities of nylon and cotton gill nets for ciscoes, chub spp., yellow perch, and white suckers. These studies were carried out on catches made in South Bay (45°37′ N., 81°54′ W.) and Georgian Bay (44°30′ to 46°00′ N., 80°00′ to 81°40′ W.). The catches were made from 1954 through 1959 in South Bay and in 1958 and 1959 in Georgian Bay.

METHODS

In South Bay the fish were from the same gear as was used by McCombie and Fry who give details of the mesh and cord size. Both cotton and nylon nets were used in South Bay. Similar nets were used in Georgian Bay except that these were nylon only and a 50-yard net of 1-inch stretched mesh of 140/2 thread 60 meshes deep was added to this string in 1959.

The procedures of sampling the catch and measuring the specimens were continued as described by McCombie and Fry; however, an improved method of girthing was devised (Berst and McCrimmon, 1961) and used in this study. The data were also treated in the same manner as described by the authors above, except as noted hereafter.

Although several species were captured both in South Bay and Georgian Bay, each population was treated separately because there were local differences in form. The length : weight relation in the cisco differed in the two populations, with the Georgian Bay specimens being consistently heavier (Figure 1). In addition, chi-square tests in which the frequencies for each half-inch length class for South Bay were compared with their counterparts for Georgian Bay indicated significant differences in net selection between experimental gill-net catches from the two areas. These differences, however, are in selection with respect to length. If the fish are classified by girth the differences in selection disappear.

In the cases of the cisco and the perch the treatment diverged from that of McCombie and Fry in that a better linear fit of the length : girth relation was obtained between the length and the logarithm of the girth than was obtained from the arithmetic plot. Figure 2 shows data for the cisco on a semi-logarithmic plot. Satisfactory linear fits were obtained from arithmetic plots for the other species in agreement with the findings of Margetts (1954) and McCombie and Fry (1960).

SELECTIVITY AND EFFICIENCY OF NYLON GILL NETS

The equations derived for the length : girth relations of the various populations are given

[1] From a thesis for the M.A. degree, University of Toronto, 1960.

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TABLE 1.—*Formulae for the regression lines describing the length : girth relationships in the variou populations*

[x = fork length in inches; y = girth in inches]

Species	Locality	Formula	Number o specimen
Round whitefish	Georgian Bay	$y = -.2540 + .5259x$	235
Chub spp.	Georgian Bay	$y = .8729 + .4533x$	147
Cisco	South Bay	$\log y = .2841 + .0399x$	780
Cisco	Georgian Bay	$\log y = .3109 + .0376x$	182
Yellow perch	South Bay	$\log y = .2085 + .0569x$	566
Yellow perch	Georgian Bay	$\log y = .1567 + .0656x$	472
White sucker	South Bay	$y = -.4139 + .5925x$	308
White sucker	Georgian Bay	$y = -.6052 + .6169x$	257

in Table 1. The catch data are summarized in Tables 2 through 5. Figure 3 shows the result of treating the data for the round whitefish given in Table 3 by the method of McCombie and Fry. As will be seen, the scatter of the individual points is of the same order as found by them for the whitefish. Similar curves were obtained for the other groups considered here. The selection curves for the eight groups treated are shown in Figure 4.

The greatest difference between the observed and calculated distributions occurred for the sucker, the observed distribution of which is noticeably more leptokurtotic than the calculated one. A tendency to greater leptokurtosis is also apparent in the perch curves.

There is close agreement between the observed values for the girth : mesh perimeter ratios for both populations of each species. This is noteworthy in view of the differences in length selection between populations of the two areas mentioned earlier. It is therefore evident that the differences between the respective length : girth relationships of the South

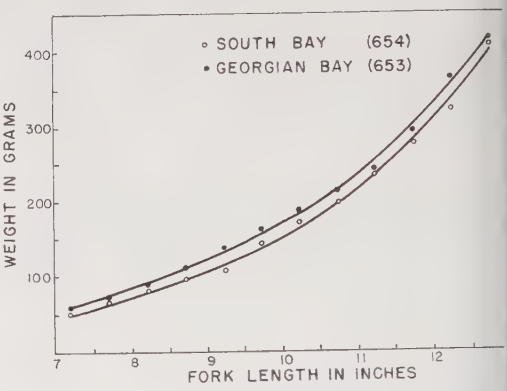

FIGURE 1.—The length : weight relationship of ci coes based on data from specimens caught in Sout Bay and Georgian Bay during 1958 and 1959. Th numbers of specimens are shown in parentheses.

Bay and Georgian Bay populations were c the appropriate order to compensate for di ferences in length selection.

The selectivity curves for the various spe cies are positively skewed. This skewness i greatest for the curves of the white suckers

TABLE 2.—*Number of ciscoes caught in experimental gangs of nylon gill nets in South Bay during the yea 1954 to 1959 and in Georgian Bay during 1958 and 1959*

[GB — Georgian Bay; SB — South Bay]

Fork length (inches)	Stretched mesh size (inches) and locality																									
	1		1–½		1–¾		2		2–¼		2–½		2–¾		3		3–½		4		4–½					
	GB		GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB				
6.5– 6.9	—		23	—	3	—	1	—	2	—	—	—	3	—	—	—	—	—	—	—	—	—				
7.0– 7.4	—		88	30	63	—	4	2	4	2	3	—	1	—	1	—	—	—	2	—	—	—				
7.5– 7.9	—		112	64	231	29	12	3	4	2	4	—	3	—	1	—	1	—	1	—	—	1				
8.0– 8.4	—		56	85	144	77	30	12	8	2	2	2	3	2	2	—	1	2	—	—	1	1				
8.5– 8.9	—		12	34	33	66	28	31	5	4	—	3	—	1	—	1	1	1	1	—	—	—				
9.0– 9.4	—		6	18	36	60	18	46	9	11	1	1	—	1	—	1	—	2	—	1	1	1				
9.5– 9.9	—		9	26	34	63	31	70	12	19	3	3	1	2	1	1	1	—	—	—	—	—				
10.0–10.4	—		9	14	53	43	78	67	41	39	3	10	2	1	1	—	—	1	—	—	—	—				
10.5–10.9	—		3	8	25	33	93	55	93	41	22	19	5	3	2	—	3	1	1	—	3	—				
11.0–11.4	—		3	1	16	11	65	38	56	59	44	23	10	9	4	—	3	2	—	1	1	—				
11.5–11.9	—		—	—	3	—	27	13	42	16	30	11	8	6	3	1	—	—	1	—	—	—				
12.0–12.4	—		—	—	—	3	7	8	15	13	9	6	4	3	3	1	—	1	—	—	—	—				
12.5–12.9	—		—	—	2	—	—	—	2	—	5	1	3	4	2	—	2	—	—	—	—	—				
13.0–13.4	—		—	—	—	—	—	—	1	—	5	1	2	—	—	1	—	—	—	—	—	—				
13.5–13.9	—		—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—	—	—	—	—				
14.0–14.4	—		—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—				

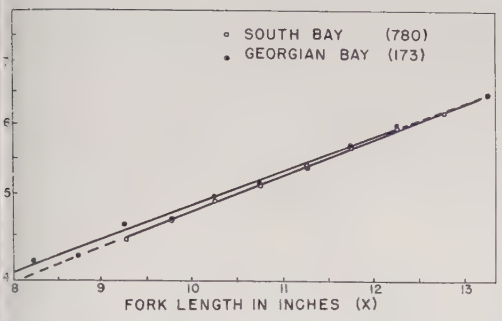

FIGURE 2.—The length : girth relationship of cis-es based on specimens caught in South Bay and orgian Bay during July and August 1959. The mbers of specimens are shown in parentheses. The es were fitted by least squares, and the respective uations are shown in Table 1.

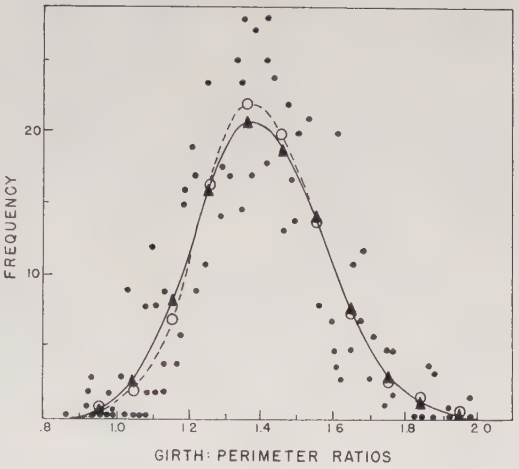

FIGURE 3.—Selectivity curve of the Georgian Bay round whitefish. The dots represent the observed frequencies adjusted on the basis that the curve for each length class encloses an area of 100 units. The dashed line (circles) is drawn through the averages of the adjusted frequencies within the various girth : perimeter ratio classes of 0.1 intervals. The solid line (triangles) is fitted by the method of moments as described by Croxton and Cowden (1959).

ith relative skewness values of 0.87 and 1.06 r the white suckers of South Bay and eorgian Bay respectively, and the least for : chubs of Georgian Bay with a value of 02.

The net-selectivity curve for each species gins to rise at a girth : mesh perimeter ratio approximately 0.8 to 0.9. It is therefore ident that the experimental gang is not ef-ctive for catching fish unless the girth of sh contacting the net is at least 80 to 90 ercent of the perimeter of the smallest mesh nd no more than 80 to 90 percent of the largest. The frequency values in the net-selectivity curves gradually decline as the girth : mesh perimeter ratio increases above that of the modal frequency. The maximum ratio at which the frequency values are negligible

ABLE 3.—*Number of chub spp. and round whitefish caught in experimental gangs of nylon gill nets in Georgian Bay during 1958 and 1959*

[A — chub spp.; B — round whitefish]

Fork length (inches)	Stretched mesh size (inches)																					
	1		1–½		1–¾		2		2–¼		2–½		2–¾		3		3–½		4		4–½		5	
	A	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
5.5– 5.9	6	15	—	—	—	4	—	—	—	1	—	—	—	4	—	4	—	2	—	2	—	—	—
6.0– 6.4	42	368	—	54	—	33	—	13	—	19	—	19	—	15	—	8	—	15	—	13	—	8	—
6.5– 6.9	66	2,564	3	489	—	125	—	98	—	44	—	62	—	45	—	29	—	32	—	35	—	26	—
7.0– 7.4	108	5,702	7	2,495	1	281	—	142	—	86	—	127	—	53	—	61	—	59	—	56	—	20	—
7.5– 7.9	54	3,021	—	3,925	—	411	—	76	—	62	—	82	—	20	—	37	—	15	—	31	—	8	—
8.0– 8.4	32	1,061	—	2,781	—	843	—	108	—	29	—	36	—	10	—	14	—	11	—	8	—	2	—
8.5– 8.9	—	167	6	517	9	668	—	148	—	44	—	15	—	4	—	2	—	1	—	4	—	10	—
9.0– 9.4	—	33	9	166	12	333	—	133	—	51	—	20	—	5	—	3	—	1	—	—	—	2	—
9.5– 9.9	—	21	3	122	28	105	8	77	2	40	—	12	—	4	—	1	—	—	—	1	—	—	—
10.0–10.4	—	5	—	54	18	32	11	68	1	55	—	28	—	5	—	1	—	2	—	—	—	—	—
10.5–10.9	—	—	—	8	7	22	8	31	5	28	—	20	1	—	—	—	—	—	—	—	—	—	—
11.0–11.4	—	—	—	—	1	5	7	8	3	26	1	12	—	3	—	—	—	—	—	—	—	—	—
11.5–11.9	—	11	—	54	4	2	7	3	5	5	2	6	—	5	—	2	—	—	—	—	—	—	—
12.0–12.4	—	—	—	—	1	1	3	—	7	5	2	4	—	3	—	2	—	—	—	—	—	—	—
12.5–12.9	—	—	—	—	—	—	5	—	6	2	2	1	1	5	—	3	—	—	—	—	—	—	—
13.0–13.4	—	—	—	—	—	—	3	1	7	—	10	2	7	—	1	1	—	—	—	—	—	—	—
13.5–13.9	—	—	—	—	—	—	7	—	4	—	2	—	5	2	4	1	1	—	—	—	—	—	—
14.0–14.4	—	—	—	—	—	—	7	—	8	1	7	—	9	1	7	—	2	—	3	—	1	—	—
14.5–14.9	—	—	—	—	—	—	3	—	9	—	6	1	17	1	19	—	2	—	1	—	—	—	—
15.0–15.4	—	—	—	—	—	—	1	—	6	—	14	—	29	1	14	—	8	—	3	—	1	—	—
15.5–15.9	—	—	—	—	1	—	3	—	7	—	9	—	27	—	13	—	12	—	6	—	—	—	2
16.0–16.4	—	—	3	—	2	—	1	—	4	—	5	—	20	—	16	—	13	—	9	—	1	—	—
16.5–16.9	—	—	—	—	—	—	—	—	3	—	2	—	6	—	14	—	15	—	6	—	—	—	—
17.0–17.4	—	—	—	—	—	—	1	—	—	—	1	—	2	—	2	—	13	—	5	—	1	—	2
17.5–17.9	—	—	—	—	1	—	—	—	—	—	2	—	1	—	—	—	3	—	2	—	—	—	—
18.0–18.4	—	—	—	—	—	—	1	—	1	—	2	—	1	—	—	—	4	—	2	—	—	—	—
18.5–18.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	—	—	—	2
19.0–19.4	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—

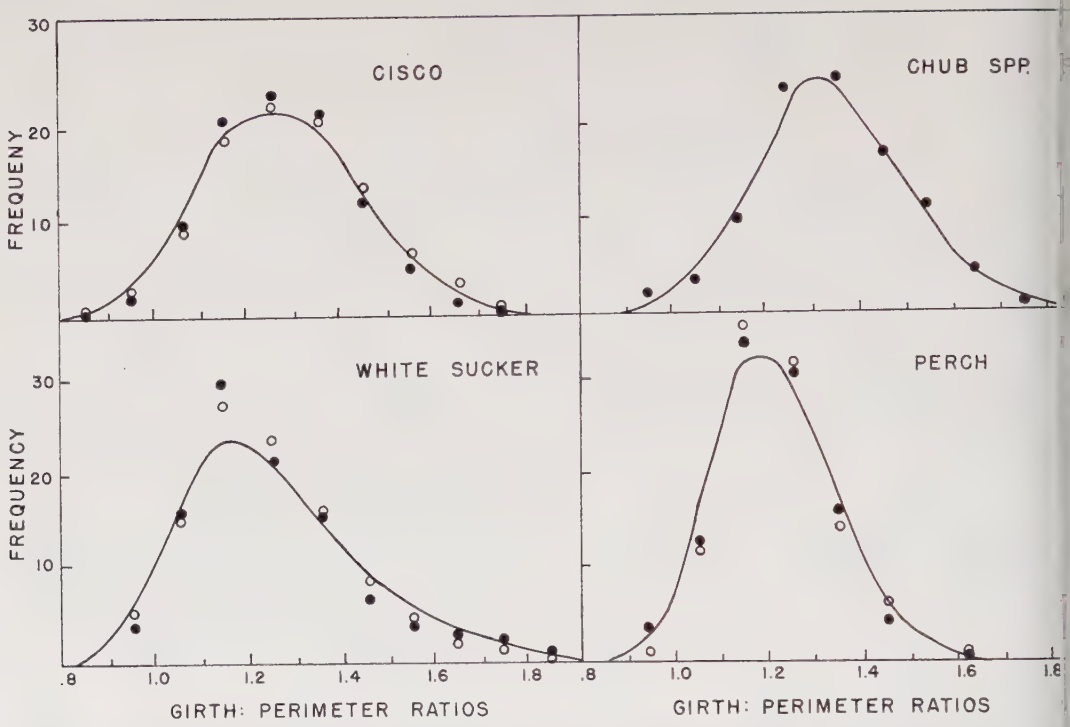

FIGURE 4.—Gill-net selectivity curves fitted by the method of moments. Those for the cisco, perch, and sucker are drawn through mean theoretical values for Georgian Bay and South Bay populations. The chub curve is for the Georgian Bay population only. The solid and open dots represent observed values for the Georgian Bay and South Bay populations respectively.

varies from approximately 1.7 for the yellow perch to 2.0 for the round whitefish. These values agree well with the value of 1.77 found by McCombie and Fry for the South Bay whitefish.

The girth : mesh perimeter ratio values for the modal frequencies (or peak catching efficiencies) for the species studied are: Georgian Bay—cisco, 1.25; round whitefish, 1.35; chub spp., 1.27; yellow perch, 1.19; white sucker, 1.15; South Bay—cisco, 1.25; yellow perch, 1.19; white sucker, 1.16. These values compare reasonably well with 1.25 for the South Bay whitefish (McCombie and Fry, 1960) and with 1.25 for the herring and the roach (Andreev, 1955). They differ considerably, however, from the 1.08 ratio value of Holt[3] for the Fraser River sockeye.

Net-efficiency correction tables for the various species may be prepared by calculating frequency values of the selectivity curves for the appropriate girth : mesh perimenter ratios. The sum of these values in a given length class may be considered an index of the relative gang efficiency for that particular class. These indices may be applied to catch data to compensate for the varying efficiencies of the net gang for the various classes of a particular species.

COMPARATIVE EFFICIENCIES OF NYLON AND COTTON GILL NETS

The catch efficiencies of nylon and cotton gill nets for the taking of ciscoes, chubs, yellow perch, and white suckers were compared for the years 1954 to 1956 inclusive. The nylon nets were generally more effective than cotton nets. The ratios of catches in nylon to those in cotton for the various species were: ciscoes, 1.33:1; chub spp., 1.49:1; yellow perch, 1.73:1; white sucker, 3.60:1.

The size composition of the catch of the nylon-net gang was compared with that of the cotton gang for each of the above species by means of 2 by 2 contingency tests (*i.e.*, length of fish × mesh size). These tests indicated a

[3] Holt, S. J. (1957) A method of determining gear selectivity and its application. ICNAF-ICES-FAO Joint Scientific Meeting, Paper No. S15, 21 pp. (Mimeo.)

TABLE 4.—*Number of yellow perch caught in experimental gangs of nylon gill nets in South Bay during the years 1954 to 1959 and in Georgian Bay during 1958 and 1959*

[GB — Georgian Bay; SB — South Bay]

Fork length (inches)	Stretched mesh size (inches)																					
	1	1–½		1–¾		2		2–¼		2–½		2–¾		3		3–½		4		4–½		5
	GB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB
4.5– 4.9	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.0– 5.4	—	350	188	3	21	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—
5.5– 5.9	6	433	1,301	159	55	—	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—
6.0– 6.4	—	265	2,453	486	842	5	27	—	—	1	1	—	—	—	—	—	—	—	—	—	1	—
6.5– 6.9	—	73	1,447	606	1,708	68	86	—	1	—	1	—	1	—	—	—	—	—	—	—	—	—
7.0– 7.4	—	12	353	371	1,341	122	322	17	2	2	1	1	—	—	—	—	—	—	—	—	—	—
7.5– 7.9	—	6	56	86	385	135	625	27	9	—	1	5	—	—	1	—	—	—	—	—	—	—
8.0– 8.4	—	—	3	7	82	22	309	31	72	12	4	4	—	—	—	—	—	—	—	—	—	—
8.5– 8.9	—	—	—	—	24	17	144	20	98	16	32	3	—	—	—	—	—	—	—	—	—	—
9.0– 9.4	—	—	—	—	8	2	48	8	76	18	53	5	1	1	—	1	—	—	—	—	—	—
9.5– 9.9	—	—	—	—	—	1	7	2	33	9	50	7	7	2	—	—	—	—	—	—	—	—
10.0–10.4	—	—	—	—	—	—	1	—	12	3	23	8	17	9	1	—	—	—	—	—	—	—
10.5–10.9	—	—	—	—	—	—	—	—	—	1	3	3	6	2	2	1	—	—	—	—	—	—
11.0–11.4	—	—	—	—	—	—	—	—	2	—	5	—	6	3	4	2	—	1	—	—	—	—
11.5–11.9	—	—	—	—	—	—	—	—	4	—	—	—	1	—	1	1	1	—	—	—	—	—
12.0–12.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	—	1	—	—	—	—
12.5–12.9	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—

high degree of correlation between the size compositions of the nylon- and cotton-net catches of the ciscoes and the chubs, a relatively low but significant correlation for the respective catches of the white sucker, but a significant difference between the numbers of yellow perch of various sizes caught by the nylon and cotton nets. The cotton nets were more efficient for the smaller sizes of perch, while the nylon nets were more efficient for the larger ones.

ACKNOWLEDGMENTS

The data were obtained from the records of the South Bay Fisheries Research Station of the Ontario Department of Lands and Forests, and Dr. W. J. K. Harkness provided the opportunity to carry out the field work. The writer is indebted to Dr. A. McCombie of the Division of Research for his assistance during the collection of data and the preparation of the original manuscript. Dr. F. E. J. Fry gave valuable direction and guidance during all phases of the study. Special thanks are due to Mr. John Budd and the staff of the Research Station without whose cooperation the study could not have been made.

TABLE 5.—*Number of white suckers caught in experimental gangs of nylon gill nets in South Bay during the years 1954 to 1959 and in Georgian Bay during 1958 and 1959*

[GB — Georgian Bay; SB — South Bay]

Fork length (inches)	Stretched mesh size (inches)																					
	1	1–½		1–¾		2		2–¼		2–½		2–¾		3		3–½		4		4–½		5
	GB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB	SB	GB
6.5– 6.9	—	—	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.0– 7.4	—	—	3	—	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.5– 7.9	—	—	1	—	30	2	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.0– 8.4	—	—	—	—	10	8	21	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
8.5– 8.9	—	—	—	—	1	3	34	1	9	—	—	—	—	—	—	—	—	—	—	—	—	—
9.0– 9.4	—	—	—	3	6	2	15	4	19	—	—	—	—	—	—	—	—	—	—	—	—	—
9.5– 9.9	—	3	—	—	—	7	15	11	24	9	21	2	—	—	—	—	—	—	—	—	—	—
10.0–10.4	—	3	—	—	4	7	12	13	39	28	45	3	29	—	8	—	2	—	—	—	—	—
10.5–10.9	—	—	2	—	—	4	—	12	18	15	26	15	16	4	9	—	—	—	—	—	—	—
11.0–11.4	—	—	—	—	—	5	4	3	3	16	38	22	26	—	16	—	—	—	—	—	—	—
11.5–11.9	—	—	—	—	—	1	4	—	12	11	19	17	43	11	19	—	—	—	—	—	—	—
12.0–12.4	—	—	1	—	—	2	4	4	—	8	22	11	23	14	14	8	1	—	—	—	—	—
12.5–12.9	—	—	—	—	—	—	—	2	2	2	3	5	14	12	13	14	6	—	—	—	—	—
13.0–13.4	—	—	—	—	—	—	—	3	—	1	8	10	15	17	11	39	10	7	—	—	—	—
13.5–13.9	—	—	—	—	—	4	—	2	2	2	7	9	14	19	20	51	28	9	4	1	—	—
14.0–14.4	—	—	—	—	1	1	3	2	8	5	6	8	20	10	20	45	58	13	2	—	—	—
14.5–14.9	—	—	—	—	—	—	—	—	4	1	3	5	7	9	20	48	68	20	15	6	2	—
15.0–15.4	—	—	—	—	—	1	—	—	2	3	2	6	13	11	12	26	57	31	51	9	1	—
15.5–15.9	—	—	—	—	—	1	3	—	—	3	1	5	11	6	9	2	51	25	60	11	8	—
16.0–16.4	—	—	—	—	—	—	—	—	3	—	1	2	4	1	6	16	22	13	46	11	16	—
16.5–16.9	—	—	—	—	—	—	—	—	—	—	—	—	3	3	1	14	12	2	31	8	16	—
17.0–17.4	—	—	—	—	—	—	—	—	—	4	—	—	—	—	1	—	5	2	24	3	15	4
17.5–17.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	6	7	—	16	—
18.0–18.4	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	1	—	8	—
18.5–18.9	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	1	1	1	3	4
19.0–19.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	4	—

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Incidence of the Giant Trematode, *Hirudinella marina* Garcin, in Skipjack Tuna, *Euthynnus pelamis* (Linnaeus), from Marquesan and Hawaiian Waters[1]

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ABSTRACT

The greater incidence of the giant trematode, *Hirudinella marina* Garcin, in skipjack tuna, *Euthynnus pelamis* (Linnaeus), from Hawaii than in skipjack from the Marquesas led to the hypothesis that this difference in infestation was due to area. Comparisons with respect to sex, size, and time led to the conclusion that a major source of variation could be attributed to time. The available data did not allow a conclusion on whether or not a real difference exists between the two areas.

INTRODUCTION

During 1956 and 1957 the staff of the Honolulu Biological Laboratory, U. S. Bureau of Commercial Fisheries, conducted an investigation of the response of skipjack tuna, *Euthynnus pelamis* (Linnaeus), to live bait in the region of the Hawaiian Islands (Yuen, 1959). During 1957 and 1958 a survey was made of the "surface" tuna resources in the region of the Marquesas Islands in northeastern French Oceania. Studies of stomach contents of skipjack tuna were important to both of these investigations. While examining the data, it was noticed that the incidence of the giant trematode, *Hirudinella marina* Garcin, was apparently considerably higher in skipjack stomachs from Hawaii than in those from the Marquesas. Analyses of the data, however, revealed no conclusive difference in infestation rates between these two areas. The results of analyses showing differences associated with other factors such as size, sex, and time are presented below.

METHODS

Stomach samples were collected from skipjack caught by the live-bait method (June, 1951). The stomachs were removed intact and placed in white muslin bags with appropriate labels and then placed in 10-percent formalin. Stomachs distended with food were split in order to facilitate preservation. Field data included the time and locality of capture, total length (as defined by Marr and Schaefer, 1949), and the sex of the fish.

Sampling in the Marquesas was carried out from U. S. Bureau of Commercial Fisheries' research vessels. From January 1957 to November 24, 1957, samples were obtained from five females from each school fished. From November 24, 1957, to the end of the survey in the Marquesas, 10 were obtained from each school, five from females and five from males. When fewer than 10 fish were caught, samples were obtained from the entire catch. In Hawaii all of the skipjack sampling was carried out from commercial fishing vessels. During the initial phases of the study, 20 samples were taken from each school whenever possible. Later the number was reduced to 10. No attempt was made to obtain equal representation of the sexes. The Marquesan samples were obtained within a radius of 250 miles from the island of Nuku Hiva, while those from Hawaii were obtained within a radius of 150 miles from the island of Oahu.

Comparisons between infestation rates were made by chi-square tests (Snedecor, 1956). The hypothesis of no difference was rejected if the probability of chi-square was less than 0.05.

IDENTIFICATION OF TREMATODE

Representatives of the genus *Hirudinella*, digenetic trematodes belonging to the family Hemiuridae, have been reported from the stomachs of a number of scombriform fishes. Depending upon the state of contraction, they may be less than 2 and greater than 5 centimeters in length, but most of our preserved specimens were between 2 and 5 centimeters. Their life cycle is presently unknown.

The genus has been studied in detail by Nigrelli and Stunkard (1947). They ascribed the giant trematodes from the wahoo, *Acanthocybium solanderi* (Cuvier and Valencien-

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nes), to *H. ventricosa* (Pallas). Although uncertainty was expressed about the identification of the giant trematodes found in other hosts, they considered them to belong to a single species, *H. marina* Garcin, on the basis of various morphological differences from *H. ventricosa.* The hosts of *H. marina* included the following species of scombriform fishes: *Parathunnus atlanticus* (Lesson), *Katsuwonus pelamis* (Linnaeus), *Euthynnus alletteratus* (Rafinesque), *Neothunnus macropterus* (Temminck and Schlegel), *Makaira mitsukurii* (Jordan and Snyder), *Scomberomorus maculatus* (Mitchill), and *Thunnus thynnus* (Linnaeus).

SINGLE AND MULTIPLE OCCURRENCES

H. marina was found in 311 of the 1,130 skipjack tuna stomachs examined. One trematode per stomach was most common. Only eight of the stomachs had more than two trematodes. The highest number found in a single stomach was four (Table 1). Although Iversen and Yoshida (1957) found as many as 17 *H. ventricosa* in a single wahoo stomach, they reported two *H. ventricosa* per stomach as the most common occurrence.

Trematodes occurred more often in skipjack stomachs collected in Hawaiian waters than in those collected in Marquesan waters (Table 1). Chi-square tests showed the differences between the two areas to be significant in the total number of stomachs infested ($\chi^2 = 26.434$; $p < 0.0001$) and also in the number of stomachs containing one trematode ($\chi^2 = 20.412$; $p < 0.0001$), but nonsignificant in the number of stomachs containing more than one.

The percentages of trematode occurrences, 20.6 percent for Marquesan skipjack and 34.3 percent for Hawaiian skipjack, are similar to those for other tunas caught in central Pacific waters. King and Ikehara (1956: page 66) found 32 percent of 166 bigeye (*Parathunnus sibi*) and 26 percent of 439 yellowfin (*Neothunnus macropterus*) with the trematodes in their stomachs. These trematodes were stated very likely to be *H. marina* by Iversen and Hoven (1958). These rates contrast sharply with the incidence of *H. ventricosa* in 98.2 percent of 220 wahoo caught in the area of the Line Islands (Iversen and Yoshida, 1957).

INCIDENCE BY SEX

The infestation rates for males and females from the two areas showed a significant difference between sexes for Marquesan skipjack tuna ($\chi^2 = 17.765$; $p < 0.0001$), but not for Hawaiian. Examination of the data indicated that this difference was probably due to the high incidence in the exclusively female samples obtained in January, February, and March of 1957. When the comparison was based on data only from those months in which both sexes were represented, the difference between sexes within the Marquesas (15.0 percent for females and 10.8 percent for males, Table 2) was not significant. Comparison within months of the infestation rates between sexes showed no significant differences in the months during which both sexes had been sampled for either Marquesan or Hawaiian skipjack.

Separation of the data into length groups from schools which had both sexes sampled (Table 2) revealed significant differences between sexes for only the 40.0–49.9-centimeter Marquesan skipjack ($\chi^2 = 4.472$; $p < 0.05$). The rest of the length groups for the Marquesan area and all for the Hawaiian area showed no significant difference between sexes.

Comparison of the incidence of trematodes in the same sex from the two areas showed significant differences. The 21 out of 195 for the Marquesan male skipjack was significantly less than the 91 out of 280 for the Hawaiian male skipjack ($\chi^2 = 29.761$; $p < 0.0001$), as was the 94 out of 363 for Marquesan female skipjack from the 92 out of 261 for Hawaiian female skipjack ($\chi^2 = 6.366$; $p < 0.02$).

While making the above comparisons, the

TABLE 1.—*Summary of single and multiple occurrences of giant trematodes in stomachs of skipjack tuna from the Marquesas and Hawaii*

[Percentage occurrences in parentheses]

Area	Number of stomachs examined	Number of stomachs containing:					Total number of stomachs containing trematodes
		0 Trematode	1 Trematode	2 Trematodes	3 Trematodes	4 Trematodes	
Marquesas	558	443 (79.4)	75 (13.4)	37 (6.6)	3 (0.5)	0 (0)	115 (20.6)
Hawaii	572	376 (65.7)	137 (24.0)	54 (9.4)	4 (0.7)	1 (0.2)	196 (34.3)

TABLE 2.—*Giant trematode incidences in stomachs of male and female skipjack tuna of various lengths from the Marquesas and Hawaii*

Item	Length group (centimeters)						Total
	30.0–39.9	40.0–49.9	50.0–59.9	60.0–69.9	70.0–79.9	80.0–89.9	
			Marquesas[1]				
Male							
Number of stomachs	—	104	55	5	29	2	195
Number with trematodes	—	5	10	1	4	1	21
Percentage infestation	—	4.8	18.2	20.0	13.8	50.0	10.8
Female							
Number of stomachs	1	124	40	6	27	2	200
Number with trematodes	0	16	9	1	4	0	30
Percentage infestation	0	12.9	22.5	16.7	14.8	0.0	15.0
Both sexes							
Number of stomachs	1	228	95	11	56	4	395
Number with trematodes	0	21	19	2	8	1	51
Percentage infestation	0	9.2	20.0	18.2	14.3	25.0	12.9
			Hawaii[2]				
Male							
Number of stomachs	1	29	31	16	159	18	254
Number with trematodes	0	4	14	9	49	6	82
Percentage infestation	0	13.8	45.2	56.2	30.8	33.3	32.3
Female							
Number of stomachs	—	25	32	20	155	5	237
Number with trematodes	—	5	13	10	56	2	86
Percentage infestation	—	20.0	40.6	50.0	36.1	40.0	36.3
Both sexes							
Number of stomachs	1	54	63	36	314	23	491
Number with trematodes	0	9	27	19	105	8	168
Percentage infestation	0	16.7	42.9	52.8	33.4	34.8	34.2

[1] Data from schools which did not have both sexes sampled are not included.
[2] Length data for 60 samples were not available. Ten of these plus 21 others had no sex data available.

magnitude of the between-year difference, particularly of females in the Marquesas, was noticed. Since the data from the two areas did not cover the same period of time, it was necessary to determine whether differences existed between years within sexes of the same area. For the Marquesas the incidence of trematodes in females during 1957 was significantly greater than that in the females during 1958 ($\chi^2 = 35.852$; $p < 0.0001$). Comparable data were unavailable for males. For Hawaii no yearly differences were found for females, but for males a significant difference was found between 1956 and 1957 ($\chi^2 = 7.907$; $p < 0.01$).

INCIDENCE BY SIZE

Since there was only one length group which showed a significant difference between sexes (the 40.0–49.9-centimeter group for the Marquesas), the data for the two sexes were combined for comparisons between length groups. No significant difference was observed between sizes in the Marquesas, but a significant difference was observed for Hawaii ($\chi^2 = 15.060$; $p < 0.005$). As seen in the data tabulated in the lines labeled "Both sexes" in Table 2, there was a higher incidence in the Hawaiian skipjack than in Marquesan skipjack for each length group. Significant differences between the same length groups from the two areas were observed for the 50.0–59.9-($\chi^2 = 9.652$; $p < 0.003$), 60.0–69.9-($\chi^2 = 4.215$; $p < 0.05$), and 70.0–79.9-($\chi^2 = 8.250$; $p < 0.005$) centimeter groups.

INCIDENCE BY SEASON AND YEAR

To make seasonal comparisons of trematode incidences, the data were divided into "season" and "off-season" (Table 3). The season months for Hawaii include May, June, July, August, and September, since the highest catch from the commercial fishery for Hawaiian skipjack occurs during these months (Yamashita, 1958). Similar seasonal catch data are not available for the Marquesan region, because a commercial fishery does not exist there. Wilson and Austin (1957), however, have reported that more than three times as many skipjack schools were sighted in the Marquesas during the southern hemisphere summer as during the southern hemisphere winter. Data for the months of November, December, January, February, and March were combined and designated as the "season" period for the Marquesan region. The remaining months were lumped together as the "off-season" for each of the areas.

No significant seasonal differences were found within the same years and same areas. When the 1957 season was compared with the 1958 season (Table 3) for the Marquesas, however, a significant difference was observed

TABLE 3.—*Seasonal and yearly variations of giant trematode incidences in stomachs of skipjack tuna from the Marquesas and Hawaii*

Item	Year			Total
	1956	1957	1958	
Marquesas				
Season				
Number of stomachs	—	128[1]	283	411
Number with trematodes	—	57	38	95
Percentage infestation	—	44.5	13.4	23.1
Off-season				
Number of stomachs	—	15[1]	132	147
Number with trematodes	—	4	16	20
Percentage infestation	—	26.7	12.1	13.6
Hawaii				
Season				
Number of stomachs	383	129	—	512
Number with trematodes	117	57	—	174
Percentage infestation	30.5	44.2	—	34.0
Off-season				
Number of stomachs	40	20	—	60
Number with trematodes	16	6	—	22
Percentage infestation	40.0	30.0	—	36.7

[1] These samples were from female skipjack only.

($\chi^2 = 47.708$; $p < 0.0001$), as was the case for the Hawaiian area when the 1956 season was compared with the 1957 season ($\chi^2 = 7.808$; $p < 0.01$). Differences between the off-seasons of 1957 and 1958 for the Marquesas and of 1956 and 1957 for Hawaii were not significant. For the Marquesas data, it is possible that the difference between seasons may have been influenced by the nonrepresentation of males in the 1957 samples. Accordingly, the 1958 data for male skipjack were eliminated. The season difference for 1957 and 1958 was still significant ($\chi^2 = 26.895$; $p < 0.0001$). The off-season difference was not. Comparison of season ($\chi^2 = 12.598$; $p < 0.0005$) and off-season ($\chi^2 = 13.923$; $p < 0.0003$) totals showed that the trematode incidences in Hawaiian skipjack were significantly higher than in Marquesan skipjack. When the data were rearranged and examined for differences between years within the same length group and within the same area, significant differences were found in three length groups from the Marquesas: 40.0–49.9-centimeter ($\chi^2 = 13.494$; $p < 0.0003$), 50.0–59.9-centimeter ($\chi^2 = 4.334$; $p < 0.05$), and 60.0–69.9-centimeter ($\chi^2 = 9.892$; $p < 0.003$). For the area of Hawaii, only one length group, 60.0–69.9-centimeter ($\chi^2 = 5.730$; $p < 0.03$), showed a significant yearly difference.

The results to this point led to a final comparison, a between-area, within-year comparison, for which only the 1957 data could be used. The difference was not significant.

DISCUSSION AND CONCLUSION

The contrast in the trematode incidence between Hawaiian skipjack tuna and Marquesan skipjack tuna led to the hypothesis that this difference was due to area. Significant differences revealed by the following comparisons supported the hypothesis: males and females from the Marquesas versus those from Hawaii, length groups from the Marquesas versus corresponding length groups from Hawaii (for the 50-, 60-, and 70-centimeter groups), and seasons and off-seasons in the Marquesas versus those in Hawaii.

Within area comparisons of the following categories, however, also yielded significant differences: females of different years in the Marquesas, males of different years in Hawaii, seasons of different years of both areas, length groups in Hawaii, and within certain length groups of different years (the 40-, 50-, 60-centimeter groups of the Marquesas and the 60-centimeter group of Hawaii). All of the differences within area are associated with time and size. Since size itself is associated with time, it appears that a major source of variation may be attributed to time. That time was a more important factor in the observed differences is supported by the data of 1957, the only year common to both areas. The difference between the two areas was not significant for that year. Regrettably, the data from the two areas, collected incidentally to other studies, do not cover the same years. Thus, they do not permit a measure of the time variable in those comparisons which show an inter-area difference.

In conclusion, the difference observed between the incidences of *Hirudinella marina* in skipjack tuna from Hawaii and from the Marquesas seems to be associated with time rather than area. Whether or not a real difference does exist between these areas could not be determined from the available data.

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Growth of Wild and Hatchery Strains of Brook Trout[1]

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ABSTRACT

Various growth characteristics of the brook trout (*Salvelinus fontinalis*) were investigated by comparing the performance of three wild populations with five hatchery groups. Wild populations attained a total length at the end of 2 years of about 6 inches, which was less than half the size of the hatchery trout in the same period. Differences in weight between wild fish and hatchery fish for the same period were of the order of 10 times. Unfavorable temperature and lack of food were chief causes of slow growth of wild populations. Among the hatchery groups, inbreeding caused a decrease in growth. Randomly bred groups were very similar in size at all times up to 20 months of age. Growth rates of brook trout decline rapidly with increase in length or weight. Total length does not increase exponentially over long time periods, but growth in length more closely approximates a linear series with time. Different mathematical models were applied to growth data from the hatchery groups. The Walford–Ford concept was not applicable because the predicted ultimate sizes of the groups were unrealistic. The concept of Parker and Larkin appeared to describe adequately the growth curves obtained and was useful in measuring differences due to genetic factors. Weight–length curves were similar for fish of different strains grown under similar environmental conditions. Inbred groups had markedly different weight–length curves from those of randomly bred groups. A modification of LeCren's relative condition factor, derived from the weight–length data of the hatchery groups of brook trout, is proposed. It compares the observed weight of a fish with the weight expected to promote the optimum rate of growth of the species. Examples of its use for wild and hatchery groups are given.

INTRODUCTION

In an earlier paper Cooper (1953) described the seasonal growth of three wild populations of brook trout (*Salvelinus fontinalis*). Large differences in growth of the trout were observed between summer and winter, and differences due to the effects of temperature and food were briefly discussed. The purpose of the present investigation was to compare the growth performance of five groups of domesticated brook trout, maintained under conditions of adequate food and favorable temperatures, with the growth of the three wild populations. The availability of different stocks of domesticated brook trout also provided an opportunity to compare growth rates between hatchery strains and between groups of different levels of inbreeding. All of these comparisons are useful in interpreting the effects of water temperature, of food supply, and of genetic constitution on growth performance.

METHODS OF STUDY

The three wild populations of brook trout studied were from streams in northern Michigan, tributary to Lake Huron. Hunt Creek is the smallest of the three, averaging about 20 feet in width; the Pigeon River averages about 40 feet wide. The North Branch of the Au Sable River is the largest of the three being about 200 feet wide. All three streams have hard water and receive an abundant supply of ground water as general seepage in the areas studied. Other details of these streams and the fish populations are given by Cooper (1953).

The five groups of domesticated brook trout were made available for study by the Pennsylvania Fish Commission at their Benner Spring Fish Research Station. All of the trout were progeny from hatchery stocks maintained under domestication for many years. Three groups (pond 90, Berlin, New Hampshire, stock; pond 98, New Jersey stock; and pond 94, Pennsylvania stock females × New Jersey stock males) originated from matings of two females with two or more randomly selected males. The other two groups came from inbreeding trout of two different hatchery strains of the Pennsylvania Fish Commission. One of the inbred groups (pond 92) was derived from mating one female with 15 of her yearling sons; the other group (pond 96) originated from a mating of two females with two of their brothers.

The trout were individually weighed and measured periodically throughout the investigation. Care was taken to select a sufficiently sensitive unit of measurement to reflect mi-

[1] Authorized for publication on November 8, 1960, as paper No. 2506 in the journal series of the Pennsylvania Agricultural Experiment Station.

or differences in the entire range observed r a particular size group. For example, the inch fish were weighed to the nearest 0.1 am, while fish over 12 inches were weighed ly to the nearest 10 grams. The length of e small fish was recorded to the nearest illimeter; fish larger than 3 inches were easured to the nearest 0.1 inch. The sex of e individual fish was not determined al- ough both sexes were well represented in e groups, as judged from observations made hen the groups matured sexually.

The domesticated groups of trout were seg- gated in similar concrete ponds and received e routine care and food accorded all the atchery fish. There were 92 fish in each oup at the beginning of the experiment on pril 30, 1957. Of these, at least 50 fish in ch group were weighed and measured at e end of each experimental period. Mortal- y was from 10 to 20 percent in a 16-month riod, except for one group which suffered mortality of an unidentified cause of about percent during the 16th month. The ex- riment was terminated because of this mor- lity on August 29, 1958.

Studies of growth of many animals have ten been pursued on a basis of gain in ight. Such a procedure has obvious advan- ges in production studies. For many fishery investigators, however, the length is often the only measurement taken, although for critical studies both length and weight are sometimes recorded. In the present study we analyzed growth chiefly on a basis of the total length of the fish with corresponding weight data given to enable other investigators to make conversions when desirable.

COMPARISON OF MEAN TOTAL LENGTHS

As a first approach to an analysis of growth, the mean total lengths of the five groups of trout were tabulated according to the dates on which samples were measured. This procedure was not entirely satisfactory because the five groups of fish were spawned at different times and began feeding at some- what different dates following absorption of the yolk sac. Their ages, therefore, differed as much as 27 days on the dates when the measurements were taken. Since it appeared impractical to measure each group separately at the end of monthly periods following the different dates of first feeding, the mean lengths of all of the groups obtained on the same calendar date were recorded (Table 1). A closer approximation to the actual growth history of the five groups is given in Figure 1, in which the mean lengths have been plotted in relation to their actual age in days

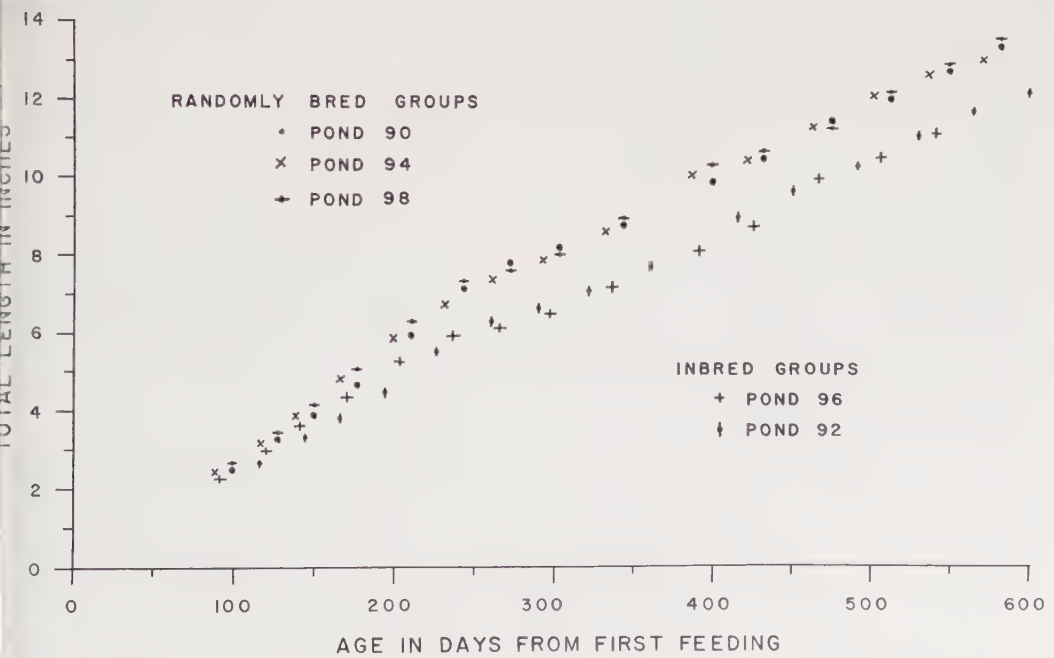

FIGURE 1.—A comparison of the growth of five groups of hatchery brook trout representing different stocks nd different degrees of inbreeding.

TABLE 1.—*Comparison of growth in total length between different groups of hatchery brook trout*

[Number of fish in each sample indicated in parentheses]

Date	Randomly bred groups						Inbred groups			
	Pond 90		Pond 94		Pond 98		Pond 92		Pond 96	
	Total length (inches)	C[1]	Total length (inches)	C	Total length (inches)	C	Total length (inches)	C	Total length (inches)	C
Apr. 30, 1957	2.50 (50)	10.0	2.45 (50)	8.6	2.54 (50)	11.4	2.67 (50)	8.2	2.39 (50)	9.6
May 28	3.23 (50)	10.2	3.19 (50)	10.7	3.38 (50)	13.0	3.36 (50)	10.4	3.01 (50)	12.3
June 19	3.91 (50)	11.0	3.86 (50)	9.8	4.18 (50)	7.9	3.81 (50)	10.0	3.61 (50)	11.6
July 17	4.62 (50)	13.9	4.82 (50)	7.7	5.05 (50)	9.5	4.48 (50)	11.2	4.38 (50)	11.6
Aug. 19	5.95 (50)	11.4	5.87 (50)	7.7	6.30 (50)	9.4	5.52 (50)	12.0	5.28 (50)	13.3
Sept. 21	7.15 (50)	10.3	6.74 (50)	9.5	7.21 (50)	9.7	6.32 (50)	11.4	5.94 (50)	13.1
Oct. 22	7.79 (50)	9.2	7.39 (50)	7.8	7.66 (50)	7.4	6.65 (50)	11.4	6.14 (50)	11.2
Nov. 23	8.19 (77)	7.9	7.85 (85)	8.3	8.13 (85)	7.9	7.12 (78)	10.5	6.51 (79)	12.1
Jan. 2, 1958	8.77 (50)	8.0	8.60 (50)	8.6	8.91 (50)	7.1	7.74 (50)	11.8	7.20 (50)	12.9
Feb. 26	9.88 (50)	7.3	10.07 (50)	7.9	10.35 (50)	6.1	8.98 (50)	9.9	8.15 (50)	13.6
Apr. 1	10.51 (50)	7.1	10.45 (50)	8.2	10.66 (50)	7.3	9.66 (50)	9.6	8.78 (50)	12.6
May 13	11.49 (50)	6.4	11.36 (50)	6.2	11.46 (50)	7.6	10.33 (50)	9.2	9.96 (50)	9.6
June 20	12.05 (50)	6.9	12.14 (50)	6.1	12.04 (50)	6.4	11.10 (50)	7.6	10.52 (50)	8.9
July 25	12.78 (50)	5.5	12.68 (50)	6.0	12.84 (50)	5.5	11.74 (50)	7.3	11.18 (46)	8.9
Aug. 29	13.41 (50)	6.1	13.05 (50)	5.3	13.40 (50)	6.6	12.42 (50)	7.0	– –	–
Date of first feeding	January 21		February 1		January 21		January 4		January 28	

[1] *C* = coefficient of variation.

from first feeding. The periods between sampling dates were approximately monthly intervals, although no special care was taken to make the time periods of equal length.

All five groups of domesticated trout grew rapidly in the favorable environment of the hatchery, reaching an average size of about 13 inches at an age of 20 months. Although no records were kept of the amount of food consumed, the fish were fed several times daily when they were small and at least once daily as they grew larger. The temperature of the water in all five raceways varied only a few degrees from 50° F. for the entire 16-month period. Mortality was low and no obvious symptoms of disease or nutritional deficiency were apparent in any of the ponds until shortly before the close of the experiment. The excellent growth of the trout under these conditions is consistent with the findings of Baldwin (1957) and Haskell, Wolf, and Bouchard (1956) that the temperature for maximum growth of this species approximates 55° F.

The trout in ponds 90, 94, and 98, constituting the randomly bred groups, showed few significant differences in mean lengths obtained at the various times when measurements were made (Table 1, Figure 1). This uniformity of growth exhibited by the Berlin stock, the New Jersey stock, and the cross-bred Pennsylvania × New Jersey stock was unexpected. Because these groups have been isolated from other hatchery stocks for many

nerations and ostensibly selected, under esumably different environmental condi-ns, for fast growth and disease resistance, was expected that they would show some herent differences in growth capacity when own under similar hatchery conditions.

The two ponds (92 and 96) containing in-ed trout likewise showed only minor differ-ces in growth, especially when compared on basis of their actual age (Figure 1). How-er, because the growth of the inbred groups ppeared to be consistently slower than the ndomly bred groups, the original data were combined into only these two categories for atistical comparison of the mean lengths. fferences in the mean lengths between se two categories were found to be highly nificant for all periods except the first 2 nths (Table 2).

The only significant differences in growth length noted in the five groups of domesti-ed trout appear to be associated with the stem of mating. It appears likely that a gh degree of heterozygosity for the capacity r growth has been obtained in all of these mesticated stocks which can be maintained random mating of females with one or re males from a group of brood fish. The sociation of heterozygosity with increased owth of many plants and animals is well own and has been well documented by rner (1954).

RATES OF GROWTH IN LENGTH

In the analysis of vital statistics of fish pulations, instantaneous growth rates have been recommended because of their utility in related calculations of biomass, although it is recognized that growth is not positively exponential over a long period in the life of a fish (Ricker, 1958). For this reason instantaneous rates of growth ideally should be used for comparatively short segments of the entire growth history. In practice, however, most growth studies have been based on calculations of length or weight on an annual basis because the scale method for determining the age of the fish is used. Such a procedure usually indicates a decrease in the instantaneous growth rate as the fish grows older or larger but necessarily assumes that growth between annual calculations is positively exponential (Gerking, 1954).

As a close approximation to the instantaneous growth rate, the specific growth rate of Brown (1946a) has been used in the present comparisons. This method expresses the rate of growth in terms of the percentage increase in length or weight per day relative to the length or weight of the fish at the beginning of the period.

The five groups of hatchery trout used in the present experiment grew as much in 1 year as many wild populations grow in 3 years. The specific rate of growth of these groups of fish over short periods of time was examined, therefore, and the differences in the growth rates between hatchery stocks and wild fish were compared. All five groups of hatchery trout exhibited a rapidly decreasing specific growth rate as the trout grew larger. As a typical example, the trout in pond 92 were growing at a rate of 0.82 percent of their length per day during the 28-day period when their length increased from 2.67 to 3.36 inches. Toward the end of the experiment, the specific growth rate of this group had declined to 0.16 percent per day during the 35-day period when their length increased from 11.74 to 12.42 inches.

The specific growth rate for the trout in pond 92, calculated for the entire 482-day period, was 0.32 percent per day, based on the assumption that the rate of growth remained constant throughout the entire period. The empirical growth curve of these fish deviates significantly from the curve calculated from the specific growth rate for this period (Figure 2). Daily increments of growth in length remained almost constant whereas the calculated curve assumes that the daily increments increase exponentially.

Larkin, Terpenning, and Parker (1957)

BLE 2.—*Comparison of the mean lengths of in-bred groups of brook trout with randomly bred groups computed from samples taken at successive dates*

Date	Inbred group (ponds 92 and 96 combined)		Randomly bred group (ponds 90, 94, and 96 combined)		Approximate value of *P*
	Mean	Standard error	Mean	Standard error	
ril 30, 1957	2.53	0.027	2.50	0.020	0.3
y 28	3.19	0.040	3.27	0.031	0.1
ie 19	3.71	0.041	3.98	0.033	0.001
y 17	4.43	0.051	4.83	0.044	0.001
gust 19	5.40	0.068	6.04	0.050	0.001
ptember 21	6.13	0.077	7.03	0.064	0.001
tober 22	6.40	0.077	7.61	0.053	0.001
vember 23	6.81	0.066	8.05	0.042	0.001
uary 2, 1958	7.47	0.096	8.76	0.057	0.001
bruary 26	8.57	0.110	10.10	0.060	0.001
ril 1	9.22	0.111	10.54	0.065	0.001
y 13	10.14	0.097	11.43	0.063	0.001
ie 20	10.81	0.093	12.08	0.064	0.001
y 25	11.47	0.099	12.77	0.059	0.001

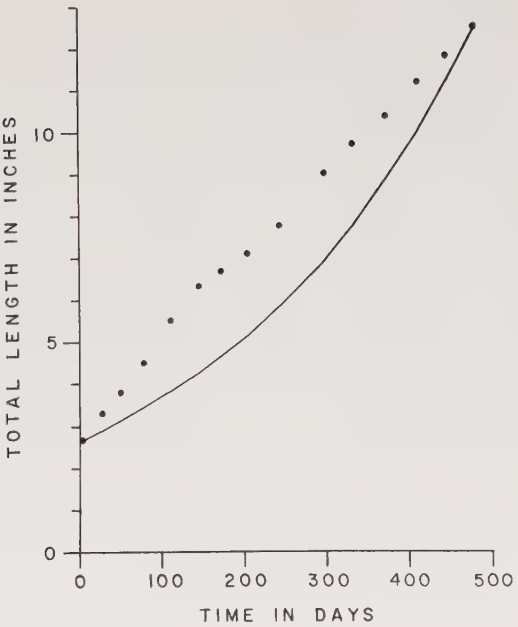

FIGURE 2.—Empirical growth of brook trout in pond 92 (dots) compared with the calculated growth curve (line) based on the average specific growth rate for the same period.

suggested the use of size-specific instantaneous growth rates for comparisons because there was a close relationship between actual size and growth rate of different populations of rainbow trout in British Columbia. A comparison of the specific growth rates of the five domesticated groups of brook trout and the three wild populations in Michigan (Cooper, 1953) also suggests that the maximum rate of growth of this species is related to the size of the fish and not its age. The wild brook trout populations studied grew to sizes of 5.9, 6.4, and 7.9 inches in a 26-month period, with the majority of the growth occurring in the early spring months. The domesticated groups reached an average size of about 13 inches in 20 months, with monthly increments of growth in length being rather uniform throughout the entire period. When comparisons of growth rate are restricted to periods of the year when conditions for growth of the wild populations are favorable, trout of equal sizes from both the wild populations and the domesticated groups had similar growth rates. There was little correlation between growth rate and age, *per se*. Since the pattern of specific growth rate is similar for both length and weight, only the figures depicting growth in weight are used (Figures 3 and 4).

The marked difference in growth pattern noted between the wild trout and domesticated fish helps to distinguish possible limiting factors in the environment. In this study the hatchery brook trout, if not closely inbred, appear to be growing at near the maximum rate under these conditions of food and temperatures. They show greater growth than wild fish for the entire year mainly because their growth starts earlier in the season due to favorable temperatures and because they grow at a relatively fast, although constantly declining, rate for the greater part of the year. This almost complete lack of a seasonal decline in growth of the hatchery trout during the fall and winter probably is due to the maintenance of sufficiently high water temperatures in the hatchery ponds to utilize available food for active growth.

Brook trout populations in natural streams in cold climates are able to grow at maximum capacity for only part of the year. During a short period in early spring, a combination of adequate food and favorable water temperatures permits the trout to grow at rates comparable to hatchery stocks. In late summer a shortage of food often is responsible for a decrease in condition and in growth even though temperatures are favorable (Cooper and Benson, 1951; Ellis and Gowing 1957). In winter, temperature usually is the limiting factor since it has been shown that although food is abundant at this time, it cannot be efficiently used for growth even if ingested (Leonard, 1942).

The interrelated effects of temperature, rate of feeding, activity, and basal metabolism on the growth of trout shown by Brown (1946c) in controlled laboratory experiments are excellent evidence of the complex interaction of factors influencing growth. At the present time, however, food, temperature, and genetic constitution appear to be the most important determinants of growth rate.

ANALYSIS OF GROWTH CURVES

Although it is well recognized that the growth of an animal is a unique, complex situation involving the interaction of many processes, the work of several investigators indicates that growth curves, when treated in different ways, may be closely simulated by mathematical models of varying degrees of complexity. A review of such information is

yond the purpose of the present work, but e reader is referred to publications of Minot 891), von Bertalanffy (1938, 1957), Brody 945), Beverton and Holt (1957), Ricker 958), and Parker and Larkin (1959) for trance to the literature on this subject. Although these methods appear to be difficult to apply to fishery investigations, they may offer a means to distinguish differences in growth capacity of fishes due to either genetic constitution or environmental factors. Alternative methods of plotting the length or

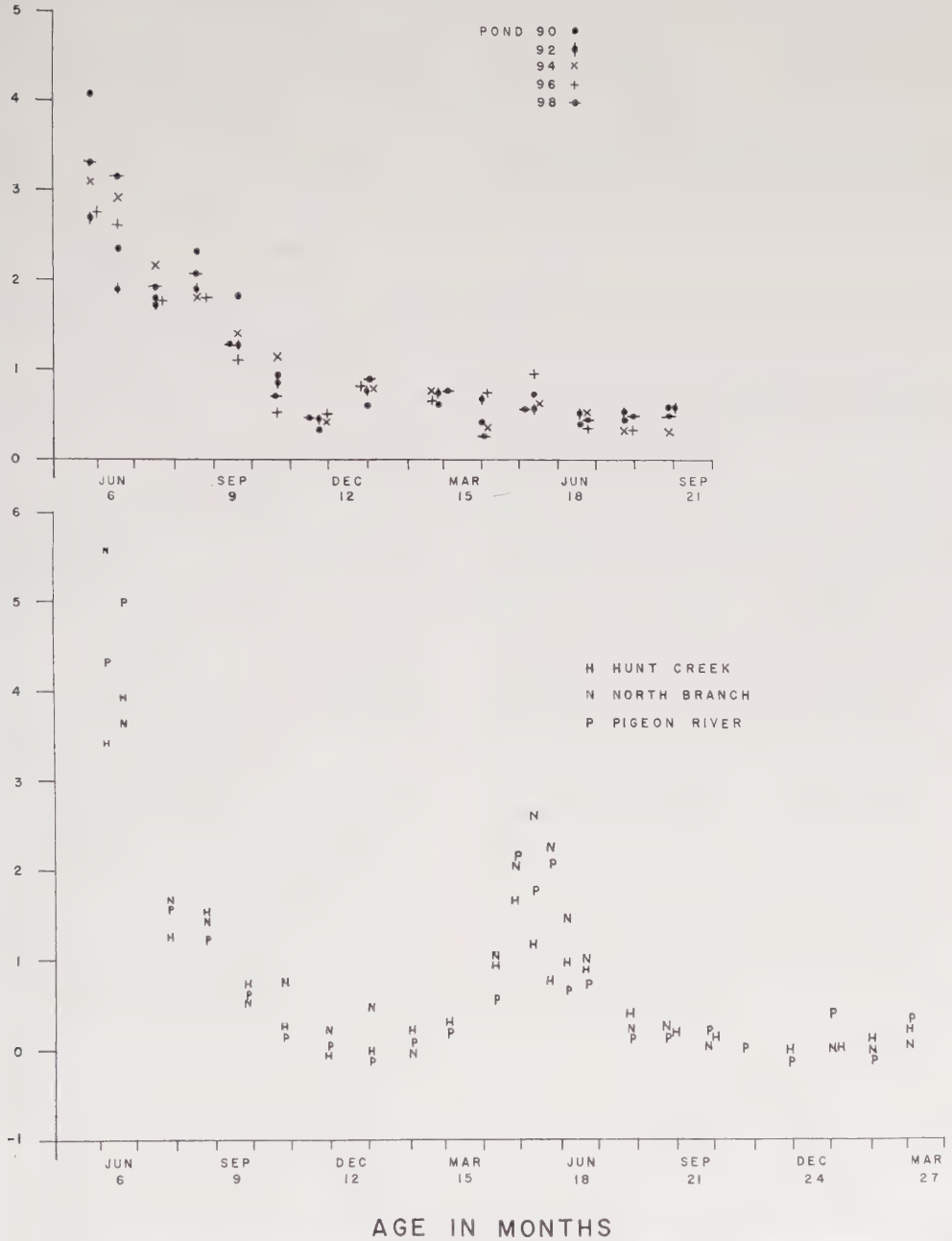

FIGURE 3.—A comparison of the specific growth rate in weight between wild and hatchery stocks of brook trout.

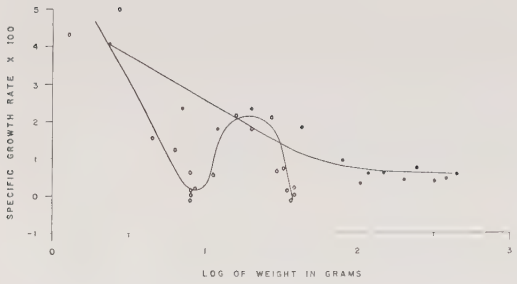

FIGURE 4.—Relationship of specific growth rate to weight of fish in wild and hatchery stocks of brook trout. Solid dots are data from pond 90; open circles are data from Pigeon River.

weight of fishes as simple time series provide little insight into the mechanism of the growth process.

The present data on growth of brook trout have been analyzed on a basis of two different concepts proposed in recent years (Walford, 1946; Parker and Larkin, 1959). These methods were chosen because they were different in concept and in ease of calculation. Both methods purport to offer possible means for distinguishing variations in growth due to inherited capability from that due to environmental factors. Application of the present data appeared to offer an additional test of the suitability of these methods because of the apparent difference in genetic growth capacity of the two groups of hatchery trout in the experiment.

As a simple graphic method of depicting a growth curve, Walford (1946) has suggested a transformation of the latter half of the typical sigmoid curve exhibited by most animals during their life history. The mathematical relationship of this method was described earlier by Ford (1933). The part of the curve below the inflection point is usually completed early in life and accounts for a very small proportion of the total growth of the animal. For the part of the sigmoid curve above the inflection point, Walford's method of plotting size at age n against size at age $n + 1$ transforms a generally depressed curve into a straight line. This line has a slope of less than 1 and intersects the 45-degree diagonal drawn through the 0, 0 origin. According to Walford, two constants, characteristic of this transformation, may be derived and used to distinguish between races or populations of animals exhibiting different growth curves. These constants are: k, which describes the slope of the transformed line; and $l\infty$, which describes the asymptotic length, or maximum size attained by the animal.

In the usual application to fish populations the size at different ages is computed from measurements of scales or bones. Thus only a few points on the curve, representing size at successive years of age, are possible. Felin (1951), however, has applied this method to growth analysis of a poeciliid fish using short time intervals and states that such a method is useful in distinguishing genotypic growth differences from differences in growth caused by environmental factors.

A comparison of transformed growth curves of the domesticated groups of trout was considered desirable for several reasons. First, the growth curves exhibited by the domesticated groups of trout are similar to the pattern generally described by Walford (1946) in that the growth rate decreased rather uniformly as the fish grew larger. Second, the major factors in the environment such as food, temperature, space, and water quality were quite similar due to the construction features of the hatchery and the nature of the experiment. Third, two groups of different mating systems were available for comparison and these groups exhibited significantly different rates of growth (Table 2). Since the fish used by Felin (1951) were of the same genetic constitution but differed only in the environmental factors to which they were exposed, the present comparison appeared to offer a complementary test of the usefulness of the growth characteristics, k and $l\infty$.

The calculated k values of the brook trout data show only slight differences between the inbred group and the randomly bred group, being 0.987 and 0.967, respectively (Table 3). These values are well within the range reported by Felin (1951, p. 21) for one genetic strain of platies (*Platypoecilus*) as "striking stability with respect to rate of deceleration of growth." Because the biological meaning of k is obscure, the author is inclined to agree with Larkin *et al.* (1957) that in this

TABLE 3.—*Growth characteristics of the transformations of two different genetic groups of brook trout (method of Walford, 1946)*

Group of fish	Slope k	Y-intercept	Asymptote (inches)
Randomly bred groups, ponds 90, 94, 98	0.967	0.72	21.8
Inbred groups, ponds 92, 96	0.987	0.49	37.7

use and others, growth curves may not be so onveniently summarized by the use of such haracteristics.

Calculated values for the asymptotic length f the two groups of brook trout also do not ppear to be realistic. The lower value of 1.8 inches is known to be less than the length ttained by the randomly bred groups in ac- ual performance. The upper value of 37.7 nches, corresponding to a weight of approxi- nately 29 pounds, has never been remotely pproached by this species anywhere. The alculation of asymptotic lengths in this man- er of extrapolation from segments of a rowth curve seems to be questionable, there- re, even when the segment of the curve ex- nds over a large portion of the predicted ltimate size of the fish.

The growth model previously described by Walford (1946) presupposes that there is an ltimate size which is approached from the nflection point of the typical sigmoid growth urve at a constant percentage rate; *i.e.*, that

$$l_{n+1} = a + bl_n$$

here l_n and l_{n+1} are lengths of the fish at the nd of two consecutive time periods, and a nd b are constants.

Parker and Larkin (1959) propose that the arabolic equation

$$l_{t+1}^z = \alpha + l_t^z$$

e used to describe the curve of growth of ishes, where α and z are constants to be de- ived from the empirical data. It is recom- nended that the application of this model be estricted to segments of the growth curve for which empirical data are available, since many species of fish undergo physiological hanges at different times during their life istory which may radically alter their growth haracteristics. In this sense the concept of rowth proposed by Parker and Larkin 1959) agrees with the idea of Brody's (1945) "stanzas of growth" but differs from that of Walford (1946) which presupposes a uni- ormly declining rate of growth from the in- lection point to a predetermined ultimate size.

Fitting empirical data to the parabolic nodel of growth proposed by Parker and arkin (1959) involves a considerable amount of statistical calculation since the optimum alue of the exponent z may only be obtained by assuming trial values and solving for the minimum relative variance of the other con- stant α. In the present study an IBM 650 Computer combined with a For Transit Automatic Coding System was used in the computations.

In determining optimum values of z for the various groups of brook trout, mean lengths of the fish at successive 20-day intervals were first determined from the empirical growth curve of each group, and subsequently used as l_t values. This choice was necessary because records of growth of the individual fish in each group were not obtained. Since 50 or more fish of each group of 92 were measured at frequent intervals throughout the 16-month period, a very accurate picture of the growth history of each group is possible (Figure 1). Optimum values of z and α were then computed for each of the five groups of trout (Table 4).

The similarity of the z values for groups of similar levels of inbreeding is striking. The difference between the mean values of z for randomly bred and inbred groups, on the other hand, may be highly significant (Snedecor, 1956, Table 2.2.2), although the number of individual mean values of z is quite small to place much reliability in such a test of differences. These observations of the variation of z values among groups of similar and different genetic composition agree well with the proposal of Parker and Larkin (1959) that such an exponent might be determined by an inherited enzyme system and that values of α may be regulated by ecological opportunity for growth. If this latter assumption concerning the role of α is true, one would expect to find no essential differences in values of α in the present data, providing comparisons are restricted to groups having the same z values. Values of α of the three randomly bred groups were computed using a z value of 1.5. For the two inbred groups, values of α were ob-

TABLE 4.—*Values of α and z for brook trout of different levels of inbreeding grown under similar environmental conditions*

[Computations made with IBM 650 Data Processing System]

Category	z	Relative variance of α
Randomly bred		
Pond 90	1.51	0.06900
Pond 94	1.53	0.06043
Pond 98	1.52	0.07490
Inbred		
Pond 92	1.23	0.05479
Pond 96	1.20	0.04075

Test of significance of differences of mean z
Randomly bred 1.52 ± 0.00682
Inbred 1.215 ± 0.01880
$t = 15$; 4 d.f., $P < 0.001$

TABLE 5.—*Growth rates of brook trout (using mean values of α) for various groups, and tests of significance*

Randomly bred groups ($z = 1.5$)			
Mean values of α for pond			
90	94	98	Ponds combined
1.87	1.79	1.86	1.84

Randomly bred groups—Analysis of variance for growth differences			
Source of variation	d.f.	Sum of squares	Mean square
Individual	69	15.9905	0.23175
Lot mean	2	0.0824	0.04120
Total	71	16.0729	0.22638

$F = 0.0412/0.23175 = 0.18$, Probability > 0.25

Inbred groups ($z = 1.2$)			
Pond	Mean	Standard error of mean	N
92	0.712	0.03326	25
96	0.682	0.03840	22

$t = 0.59$, Probability > 0.50

tained by using a z value of 1.2. From an analysis of variance it was concluded that no significant differences in growth could be distinguished from random error within ponds of trout exhibiting similar z values (Table 5). These observations lend further support to the use of growth characteristics proposed by Parker and Larkin (1959).

A close inspection of the empirical growth curve of all five groups reveals a slight decrease in growth rate early in the fall that may be associated with the onset of maturity. Judging from the emission of sperm while fish were handled during October and November, it is known that many males became functionally mature during their first year. It is believed that some females became mature during this period also since there were apparent changes in body form. Definite information on the state of maturity of the females was not obtained during this period, however, because we did not wish to sacrifice fish or change the body weight by attempting to strip the fish of its eggs.

A comparison of the growth rate of the two combined groups between the period preceding maturity and the period following maturity was made using values of α. There was some indication of significant differences in growth between these periods, with growth declining somewhat after the fish became mature. The probabilities of differences were not high enough to be generally accepted as significant, however ($P < 0.05$; $P = 0.10$; Table 6).

WEIGHT–LENGTH RELATIONSHIP

The relationship between weight and length in fishes has been shown to be adequately described by the parabolic equation $w = al^b$, where a and b are constants to be determined empirically. While the determination of this relationship has been of much use for prediction of fish weight when length only is known, the use of such constants as definitive growth characteristics of a species has not been generally favored. Analysis of natural cisco populations in Wisconsin lakes by Hile (1936) resulted in considerable variation in values of the exponent b calculated from different samples, leading him to conclude that this exponent is not fixed either for a species or a population. LeCren (1951) reported different values of b for various life history stages of the perch of Lake Windermere. Similar variations in the value of the weight–length exponent have been reported for other species, including the brook trout, by many authors (Carlander, 1950). As will be shown below, if samples are drawn from a population in which factors affecting the weight–length relationship are variable, similar values of the exponent are not to be expected.

Conditions for growth differ in a natural

TABLE 6.—*A comparison of the growth rate (using values of α) of groups of brook trout between periods prior to maturity and after maturity*

Grouping	z	Period						t (Fisher)
		Prior to maturity			Following maturity			
		Mean	Standard error of mean	N	Mean	Standard error of mean	N	
Ponds 90, 94, 98 combined	1.5	2.04	0.112	20	1.76	0.062	52	2.19 $P < 0.05$
Ponds 92, 96 combined	1.2	0.76	0.044	16	0.67	0.029	31	1.63 $P = 0.10$

TABLE 7.—*Weight–length constants of brook trout using weight–length empirical values selected from range of values observed in natural populations*

[Weight expressed in grams, total length in inches]

Weight			Constants	
2 inches	10 inches	20 inches	log *a*	*b*
0.8	220	1,760	−1.09125	3.37
0.8	100	1,760	−1.13055	3.28
1.27	178	1,493	−0.82036	3.07
0.8	100	800	−1.00000	3.00
1.76	220	1,760	−0.65757	3.00
1.76	100	1,760	−0.69687	2.91
1.76	100	800	−0.56632	2.63

environment from one year to the next, giving rise to variations in weight of fish of the same size in different years. Thus in random samples of fish of different ages drawn from populations subjected to variable environmental growth history, variation in growth rate to environmental factors usually confounds any genetic stability of the weight–length characteristic that may be present.

The observed range in weight of brook trout of a given size is sufficient to account for the range in weight–length exponents reported, provided one assumes that samples are drawn from populations exhibiting different growth histories. Biased composite samples of short heavy fish with long light fish will result in a much different *b* value than samples of short light fish with long heavy fish. Intermediate combinations will result in intermediate *b* values (Table 7).

A large composite sample of 5,212 brook trout from Michigan ranging in size from 2.3 to 12.7 inches in total length which included variations due to sex, locality, season, year, and of wild or domesticated origin resulted in a solution of the weight–length equation of $\log w = -0.74925 + 2.99 \log l$. This sample indicated that the historically accepted cubic relationship between weight and length of brook trout would be an adequate approximation for many natural populations of this species. Such an empirical determination, however, does not permit any differentiation of effects of environment on weight–length constants from genotypic effects that may be present and may differ considerably from other samples of natural populations.

In the present study it was possible to obtain extensive data on the weight–length relationship of different groups of brook trout grown under similar environmental conditions and to compare the weight–length constants of these different groups. Two slightly different analyses of the weight–length data yielded essentially the same conclusions. In the first method an analysis of variance of the regression coefficients for the different groups was completed using the relationship $w = al^b$, where both *a* and *b* were permitted to vary empirically and the line of best fit of the regression was obtained by the method of least squares. From this analysis (Table 8) it is concluded that the differences among regressions, although very small, are somewhat greater than that expected from error alone ($F = 3.09$; $0.01\ P = 3.44$).

To determine the variance of *b* alone in the data, the value of *a* was computed from the composite of all groups. Such a procedure for calculating an approximate value of *a* does not involve a serious error since the percentage variation in weight at the time of hatching is very small when compared with the variation in weight as the fish grows larger. Thus the position of the lower end of the regression line, determined by *a*, is relatively fixed, when compared with the variation observed in the slope of the line. The value of *a* calculated from the composite group ($\log a = -0.834$) was then used in regression analysis of all five groups according to the following: $Y = bX$, where $Y = \log w$ (grams) +

TABLE 8.—*Covariance test of regression of weight on length for different groups of hatchery brook trout (both of the constants* a *and* b *permitted to vary empirically)*

Group	log *a*	Regression coefficient $b_{w\,l}$	Error of estimate sum of squares	Degrees of freedom	Mean square	*F*
Pond 90	−0.827	3.14	0.01171	33		
94	−0.816	3.13	0.00620	33		
98	−0.840	3.15	0.00309	33		
92	−0.861	3.15	0.00586	33		
96	−0.804	3.10	0.01063	33		
Sum for five samples			0.03749	165	0.00022 (Error)	3.09
Composite			0.04023	169		$0.01\ P = 3.44$
Difference among regressions			0.00274	4	0.00068	

TABLE 9. -*Covariance test of regression of weight on length for different groupings of hatchery brook trou*

[Value of log a in equation $\log w = \log a + b \log l$ assumed to be −0.834 in all groups]

Group	Regression coefficient b_{yx}	Error of estimate sum of squares	d.f.	Mean square	F
Pond 90	3.152	0.01186	34		
92	3.120	0.00745	34		
94	3.154	0.00695	34		
96	3.133	0.01199	34		
98	3.142	0.00319	34		
Sum for 5 samples		0.04144	170	0.00024 (Error)	20.79
Composite		0.06139	174		0.01 $P = 3.44$
Difference among regressions		0.01995	4	0.00499	
		Randomly bred groups			
Pond 90	3.152	0.01186	34		
94	3.154	0.06695	34		
98	3.142	0.00319	34		
Sum for 3 samples		0.02200	102	0.00022 (Error)	5.18
Composite		0.02427	104		0.01 $P = 4.82$
Difference among regressions		0.00227	2	0.00114	
		Inbred groups			
Pond 92	3.120	0.00745	34		
96	3.133	0.01199	34		
Sum for 2 samples		0.01944	68	0.00029	7.52
Composite		0.02162	69		0.01 $P = 7.04$
Difference among regressions		0.00218	1	0.00218	

0.834 and $X = \log l$ (total length in inches). Differences among the five groups were then tested by analysis of variance. In this test minor differences in values of b were found to be highly significant, with the least differences found among groups of similar mating systems (Table 9).

The results obtained by this alternate method of comparing weight–length curves, which may be a more sensitive test, agree with the results of the method discussed previously. Both methods indicate that differences in the weight–length relationship exist among the different groups of trout even when grown under similar environmental conditions. It should be pointed out, however, that the differences in values of b due to inherited factors are very small when compared with the variation in values of b obtained from fish populations exhibiting different environmental growth histories (Table 7). Computation of a standard value of b for the species, therefore, will not result in much error due to genetic differences, unless further investigation reveals a larger amount of variation of b values among different strains of hatchery brook trout. A standard value of b is likely to be comparable between different hatcheries because most production hatcheries will use randomly bred populations rather than inbred lines.

GROWTH IN WEIGHT

Many aspects of the growth in weight of the brook trout studied may be surmised by combining the data on growth in length with the data on the weight–length relationship. The present discussion therefore will only consider pertinent comparisons of growth in weight between the five groups of hatchery fish and the three wild populations in order to gain some insight into the factors limiting the growth of this species.

The domesticated groups of trout grew to be roughly 10 times as heavy as the wild fish at the end of 19 months of age (Table 10), but no clue to the reason for this difference can be derived from this comparison. If the specific growth rates in weight of hatchery trout and the wild populations are plotted against time by calendar months, or against the age of the fish, it is apparent that the wild populations are growing at rates equivalent to the hatchery fish for only short periods of time (Figure 3). In fact, the wild fish commonly lose weight (negative growth rate) during many of the winter months. The larger size of the hatchery fish at the end of

ABLE 10.—*Growth in weight of brook trout of different hatchery groups and wild populations*

Group	Average weight (grams)	
	7 months	19 months
ild populations		
Hunt Creek	3.05	23.2
Pigeon River	4.56	34.2
North Branch—Au Sable	4.04	69.8
atchery stocks		
Inbred groups		
Pond 96	15.8	278
92	16.3	418
Randomly bred groups		
Pond 94	21.6	491
98	25.0	547
90	20.0	551

y period is the result of growing at a higher verage rate for the entire period.

The specific growth rate in weight of the atchery fish declines rather uniformly with n increase in size but does not show the brupt seasonal decline of the wild populaions associated with winter periods. Because here are large differences in actual weight of ild and hatchery fish of similar ages, a comarison of the specific growth rate of these wo groups may be used to determine the reationship between growth rate and size or ge. A plot of the specific growth rate of oth wild and hatchery fish against the size f the fish at the beginning of each period Figure 4) suggests that the growth rate of his species also appears to be size-specific nd not correlated with age *per se* (Larkin *et l.*, 1957). Only one hatchery group and one ild population were plotted, but all other omparisons of hatchery and wild fish are imilar in nature. Insofar as these groups of atchery and wild fish are representative of he species as a whole, it may be concluded hat wild populations have maintained as reat a capacity for growth as the domestiated fish, despite the fact that the hatchery roups have been selected for fast growth for many generations.

CONDITION FACTORS

Many fishery biologists have felt a need for n index of condition which permits a direct omparison of the relative weight of fish of lifferent lengths. Such an index is useful in lescribing seasonal changes in weight due to lifferent levels of nutrition or other causes. Condition factors have also been used to describe differences in body shape between different groups of fishes and changes in body shape as a fish grows in length. In the latter ases, it would appear that the solution of the usual weight–length relationship, $w = al^b$, more adequately describes differences in body shape between species and changes in body shape as fish increase in length.

The methods of calculation of such condition factors have usually been derived from an assumed cubic relationship between the weight and length of a fish, $w = al^3$, sometimes with an appropriate multiplicative factor to have the index approximate unity. Hile (1936) and LeCren (1951) have adequately reviewed the derivation and uses of such indices of condition. The use of a condition factor based on the cubic relationship has met with difficulty and little favor due to the general failure of the assumed cubic relationship between length and weight of fishes to fit empirical data. Values of the exponent which approximate 3.0 are to be considered the exception rather than the rule.

Numerous other difficulties are involved in the application of such condition factors, arising from the use of different units of measurement employed, various definitions of the length of a fish, and examples of nonlinear conversion factors between the different lengths used. Consequently, it is seldom possible to compare directly published data on condition of fishes because of these differences in methods of calculation.

LeCren (1951, p. 204) has suggested a relative condition factor, based on data from the perch (*Perca fluviatilis*), which would obviate many of these difficulties mentioned above. This factor is based on the empirical weight–length relationship $w = al^b$. "In practice the length–weight relationship would first be calculated as the logarithmic formula

$$\log W = \log a + n \log L$$

and smoothed mean weights, W, for each length-group computed from this log formula or read off an accurate graph. The relative condition factors would then be calculated from the formula $K_n = \frac{W}{\hat{W}}$," where W = observed weight of a fish and $\hat{W}$ = expected weight of a fish.

LeCren obtained several different solutions to the weight–length relationship based on differences in age, sex, and state of maturity of the fish. Comparisons of the relative condition of the fish were then made on a seasonal basis within these original groupings.

The value of a relative condition factor

such as proposed by LeCren would be enhanced if expected mean weights at different lengths could be obtained which would reflect a standard physiological state for the species of fish involved. Various workers (Allen, 1940; Went and Frost, 1942; Brown, 1946b; and Cooper, 1953) have shown a high positive correlation between condition of trout and salmon and their rate of growth. For this reason, and others discussed below, it is suggested that the average weight of a sample of fish prevailing at the time of maximum growth rate be used for such a standard. Under this system a condition factor of unity would represent the average weight of a sample of fish growing under optimum conditions.

It appears reasonable to assume that a species has a maximum capacity for growth which is determined genetically. It is also reasonable to believe that growth capacity in fishes as in many other organisms is determined by a rather large number of multiple genes, and that a freely interbreeding population is likely to be highly heterozygous for these growth determining factors (Lerner, 1954). Under these conditions one might expect that the growth capacity would be fully expressed under maximum genetic heterozygosity and a combination of environmental conditions which are optimum for growth.

The uniformly fast rate of growth of three randomly bred hatchery groups of different origin and the similar weight–length relationships of these groups would appear to substantiate the assumptions above. The similarity of the size-specific growth rates of wild populations, when permitted to grow under favorable environmental conditions, with those of the hatchery groups also lends support to this argument. Until significantly greater growth rates of the species are demonstrated, a composite of the weight–length data of the three hatchery groups may be accepted as a close approximation to an optimum physiological condition of this species.

A table of expected weights ($\hat{W}$) may then be calculated for fish of different sizes (Table 11) and used in turn to compute a relative condition factor for an individual fish using the simple relationship as proposed by LeCren (1951).

SEASONAL VARIATION IN RELATIVE CONDITION

Before comparing the variation in condition (K_n) observed at different times of the year, it is desirable to indicate the amount of dispersion of individual values about the mean for samples of fish of different sizes. For this purpose frequency distributions of the condition factors of individual fish for three samples from pond 90 have been tabulated. Although the considerable amount of dispersion of values about the mean will necessitate a rather large sample for comparison of condition, the difference between means of the samples of fish of different total lengths is very small (Table 12). This makes it possible to compare the condition of fish of different sizes without the expectation of additional variation due to size.

The seasonal change in condition of the hatchery trout is very small when compared to the changes observed in wild populations (Tables 13 and 14). Groups of hatchery fish were usually within 5 percent of their expected weights at different times of the year and showed no seasonal or cyclical trend in condition. The wild groups seldom attained 90 percent of their expected weights and con-

TABLE 11.—*Table of expected weights of brook trout at different sizes*

[Weight calculated from the weight–length equation $\log w = -0.82609 + 3.154 \log l$, where w = weight in grams and l = total length in inches]

Size of fish	Proportionate parts									
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
1.0	0.149	0.202	0.265	0.341	0.431	0.536	0.657	0.796	0.953	1.13
2.0	1.33	1.55	1.79	2.06	2.36	2.69	3.04	3.42	3.84	4.29
3.0	4.77	5.29	5.85	6.45	7.08	7.76	8.48	9.25	10.1	10.9
4.0	11.8	12.8	13.8	14.9	16.0	17.1	18.4	19.7	21.0	22.4
5.0	23.9	25.4	27.1	28.7	30.5	32.3	34.2	36.1	38.2	40.3
6.0	42.5	44.8	47.1	49.5	52.1	54.7	57.4	60.2	63.0	66.0
7.0	69.1	72.2	75.5	78.9	82.3	85.9	89.5	93.3	97.2	101
8.0	105	109	114	118	123	127	132	137	142	147
9.0	153	158	164	169	175	181	187	193	200	206
10.0	213	220	226	234	241	248	256	263	271	279
11.0	287	296	304	312	322	331	340	349	359	368
12.0	378	388	398	409	419	430	441	452	464	475
13.0	487	499	511	523	536	548	561	574	588	601
14.0	615	629	643	657	672	687	702	717	733	748
15.0	764	781	797	814	831	848	865	883	901	919

TABLE 12.—*Variability of relative condition within samples of brook trout from pond 90*

Date	July 17, 1957	November 23, 1957	June 20, 1958
Mean length (inches)	4.62	8.19	12.05
Relative condition	Frequency	Frequency	Frequency
.79–0.80	1		1
.81–0.82	–	–	–
.83–0.84	–	–	1
.85–0.86	1	–	–
.87–0.88	1	–	3
.89–0.90	–	1	3
.91–0.92	–	5	5
.93–0.94	1	4	2
.95 0.96	5	7	6
.97–0.98	4	10	5
.99–1.00	7	15	7
1.01–1.02	8	10	3
1.03–1.04	7	3	6
1.05–1.06	6	13	2
1.07–1.08	2	6	2
1.09–1.10	4	–	1
1.11–1.12	3	3	–
1.13–1.14	–	–	1
1.15–1.16	–	1	1
Number	50	78	49
Mean relative condition	1.013	1.005	0.977
Standard deviation of mean	0.064	0.058	0.073

istently lost over 30 percent of their expected weight during the winter period. Much of his winter loss in weight of the wild fish was recovered within a very short period in the spring.

USE OF RELATIVE CONDITION FACTOR

The determination of a table of expected weights of a species growing at a maximum rate entails considerable work done under controlled environmental conditions. However, the advantage of being able to directly compare the differences in condition due to

TABLE 13.—*Seasonal variation in relative condition of brook trout in hatchery ponds*

Date	Pond				
	90	94	98	92	96
April 30, 1957	0.85	1.00	0.98	0.91	1.06
May 28	1.14	1.04	0.99	0.93	1.06
June 19	1.05	1.09	1.05	0.97	1.07
July 17	1.01	1.00	0.98	0.94	0.97
August 19	1.00	0.98	0.98	0.90	0.93
September 21	1.02	0.99	0.96	0.89	0.92
October 22	1.04	1.06	0.99	0.99	0.98
November 23	1.00	1.00	0.96	0.92	0.94
January 2, 1958	1.02	1.01	0.99	0.95	0.93
February 26	0.98	0.97	0.96	0.91	0.94
April 1	0.94	0.97	0.95	0.92	0.97
May 13	0.98	0.99	0.97	0.95	1.01
June 20	0.99	0.99	0.98	0.92	0.97
July 25	0.95	0.97	0.94	0.94	0.90
August 29	1.01	0.99	1.01	0.98	–
Mean condition	0.999	1.003	0.979	0.934	0.975
Mean total length (19 months)	12.78	12.68	12.84	11.74	11.18

TABLE 14.—*Seasonal variation in relative condition of brook trout from three wild populations in Michigan (Cooper, 1953)*

Date	Hunt Creek	Pigeon River	North Branch
March 28, 1951	0.75	0.70	0.75
April 13	0.88	0.78	0.82
April 26	0.87	0.80	0.82
May 10	0.87	0.91	0.90
May 24	0.86	0.87	0.92
June 7	0.88	0.84	0.96
June 21	0.85	0.83	0.91
July 26	0.85	0.84	0.87
August 23	0.87	0.79	0.85
September 26	0.80	0.74	0.81
October 25	0.84	0.75	0.84
November 29	0.76	0.72	0.72
January 2, 1952	0.69	0.67	0.70
February 1	0.71	0.65	0.67
March 4	0.72	0.64	0.69
Range	0.69–0.88	0.64–0.91	0.67–0.96
Mean length at 2 years (inches)	5.78	6.26	7.87

sex, maturity, size, season, and locality with a physiological standard appears to be worth the effort involved. In addition, investigators may use any system of measuring or weighing the fish once suitable conversion values are determined for the species. It is unlikely that the relationships between standard length and total length are sufficiently different from one place to another to necessitate separate conversion tables for different localities. If agreement can be reached on a table of expected weights and conversion values between the customary lengths employed, all biologists will benefit from such a standardization of methods.

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Food of the American Smelt in Saginaw Bay, Lake Huron[1]

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ABSTRACT

The food of 159 young-of-the-year American smelt (*Osmerus mordax*) and 256 I-group and older fish from Saginaw Bay was examined. Thirty-one stomachs from the first group and 35 from the second were empty. Collections were made by bottom trawl and gill nets at seven localities in depths of 2 to 26 fathoms on 11 dates from July 21 to November 1, 1956. The O-group smelt contained mostly crustaceans which were present in all stomachs that contained food. Copepods were taken more frequently than cladocerans. Other food items were Rotatoria, small unidentified eggs, and algal remains. Crustaceans, insects, and fish made up nearly all of the food of the I-group and older smelt. Mean percentage frequency of occurrence and percentage of total volume were: crustaceans, 71 and 36 percent; insects, 31 and 44 percent; fish, 8 and 20 percent. Most important crustaceans were cladocerans and *Mysis*, the predominant insect was *Hexagenia*, and all fish were young *Notropis* or smelt. Saginaw Bay smelt compete for food with young of all associated species and with the adults of some. They did not eat commercially exploited fish other than smelt.

INTRODUCTION

The spread of the introduced American smelt, *Osmerus mordax* (Mitchill), throughout the four upper Great Lakes (Van Oosten, 1937) and the increase of stocks in many waters to extremely high levels of abundance have given rise to questions concerning relations between this species and native fishes. It is particularly important to learn more of the role of the smelt as a competitor for food and as a predator on other fish. Studies of the food habits of smelt in the Great Lakes (Schneberger, 1937) do not indicate that the species is a predator of any consequence. Available information is limited, however, and many who are interested in the fisheries of the Great Lakes are convinced that this fish is an important predator of other species. Some believe that predation on lake trout fry by smelt was the major cause of the destruction of trout stocks in Lakes Michigan and Huron and the severe decrease of lake trout in Lake Superior. The present report on the feeding of smelt in Saginaw Bay is a contribution to our knowledge in the field. The author is grateful to the crew of the Bureau of Commercial Fisheries research vessel *Cisco* for aid in collection of data. The constructive criticism and advice offered by Ralph Hile are acknowledged.

MATERIALS AND METHODS

The present study is based on 424 smelt stomachs collected at seven localities on 11 dates over the period July 21–November 1, 1956. One hundred and fifty-nine were young-of-the-year (O-group) and 265 were I-group fish and older (Table 1, Figure 1). All O-group smelt and most older fish were taken by bottom trawls, 39 feet wide at the head rope and 35 feet long. Mesh sizes (extension measure) were 2½ inches in the forward end, 1–2 inches in the after-belly, and ½ inch in the cod end. Smelt taken at stations 6 and 7 were caught by nylon gill nets. These fish were not actually gilled but were entangled in the webbing, mostly by their teeth.

Specimens were preserved whole in 10-percent formalin and the stomachs removed in the laboratory. Occurrence of various food items was recorded for individual stomachs, but the contents were so small that individual estimates of volume could not be made. For smelt older than age-group O, data on percentage volume have been based on pooled collections of all fish taken within single calendar months. Volume measurements were made with a sedimentation (centrifuge) tube graduated to 0.1 milliliter. Volumetric study of food of young-of-the-year was not attempted. Measurements of total length were made on preserved fish and corrected for shrinkage after preservation by the empirically determined factor, 1.018.

FOOD OF O-GROUP SMELT

Crustaceans were the principal food of young-of-the-year (Table 2). The only other

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TABLE 1.—*Number of smelt stomachs collected in Saginaw Bay by date, location, depth, and type of gear*

[Location of stations shown in Figure 1]

Date 1956	Station number	Depth (fathoms)	Gear	Number of stomachs	
				0-group	Older
July 21	3	3–7½	Trawl	50	50
Aug. 7	5	10	Trawl	–	50
Aug. 8	6	13–20	Gill net	–	14
Aug. 11	2	2½–5	Trawl	48	24
Aug. 31	3	3–10	Trawl	–	36
Sept. 19	5	6½–8	Trawl	30	28
Oct. 4	5	6½–11	Trawl	–	7
Oct. 9	4	3½–11	Trawl	–	12
Oct. 14	1	2–5	Trawl	31	–
Oct. 31	5	7–10	Trawl	–	9
Nov. 1	7	24	Gill net	–	35
Total	–	–	–	159	265

items were Rotatoria, small unidentified eggs, and algal remains. Crustaceans were present in all stomachs that contained food. The copepods *Cyclops* and *Diaptomus* were most commonly taken and were about equally plentiful. The latter were taken less frequently than the former in August. Copepods of both genera appeared in fewer stomachs in September (33 and 29 percent) than in other months (44 to 88 percent).

The cladocerans, *Daphnia* and *Bosmina*, were eaten by young smelt of all four collections. Both were taken more frequently in September and October than in July and August, and all stomachs in the September sample contained *Daphnia*. *Holopedium* and *Alona* were eaten only in August and September and by small percentages (4 or 5 percent) of the fish.

The stomachs of young-of-the-year smelt contained Rotatoria in July and August only. *Keratella* was present in both months (7 and 5 percent) and *Kellicottia* in August only (8 percent). Small unidentified eggs were found in 3 of the 4 months (13 to 25 percent of the stomachs). Algal remains (often in dense mats) were eaten in all months, but the percentages were small (7 to 12 percent).

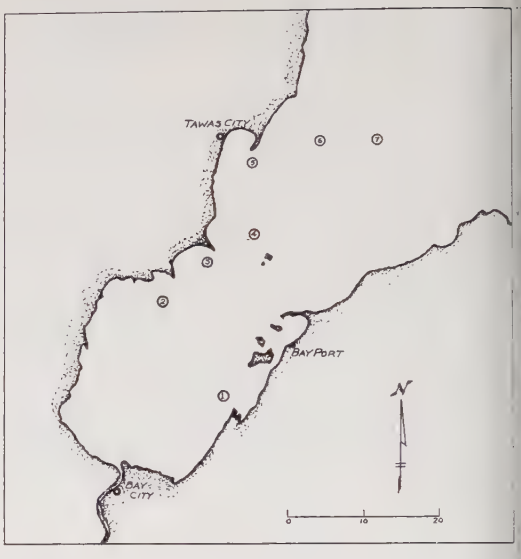

FIGURE 1.—Map of Saginaw Bay, Lake Huron, Michigan, showing location of the stations (circled numbers) at which smelt stomachs were collected.

TABLE 2.—*Food of young-of-the-year (0-group) smelt expressed in percentage frequency of occurrence*

Item	Percentage frequency			
	July 21	Aug. 11	Sept. 19	Oct. 14
Number of stomachs	50	48	30	31
Number empty	8	10	6	7
Fish length (inches)	1.1–1.9	1.2–2.3	1.7–2.3	1.7–2.5
Depth (fathoms)	2½	2½	6½–8	3
Crustacea	100	100	100	100
Copepoda				
Cyclops	76	78	33	83
Diaptomus	78	44	29	88
Cladocera				
Daphnia	19	10	100	67
Bosmina	14	8	25	42
Holopedium	–	5	4	–
Alona	–	5	4	
Rotatoria	7	13	–	–
Keratella	7	5	–	–
Kellicottia	–	8	–	–
Small eggs	17	13	–	25
Algal remains	7	8	8	12

Only limited data have been published concerning the food of young smelt. Greene (1930) found copepods, cladocerans, rotifers, and algae in small smelt collected in lakes of the Champlain watershed, New York, during the summer. In other published studies food of the large and small fish were not separated.

FOOD OF I-GROUP AND OLDER SMELT

The food of I-group and older smelt was almost exclusively crustaceans, insects, and fish (Tables 3 and 4). The only other items, Hydracarina and debris, occurred in trivial frequencies and amounts. Crustaceans were eaten most frequently; insects made up the greatest bulk of food; and fish, although present in few stomachs, made up a substantial percentage of the total diet.

Crustaceans were most prominent in the diet in July, October, and November when the percentage frequency ranged from 86 to 100 percent and the percentage volume from 25 to just under 100 percent. They were less common in August (frequency, 57 percent; vol-

BLE 3.—*Food of age-group I or older Saginaw Bay smelt expressed in percentage frequency of occurrence nd (in parentheses) percentage of total volume for each food item*

[Less than 0.5 is indicated as a trace (tr)]

Item	Percentage frequency				
	July 21	Aug. 7, 8, 11, and 31	Sept. 19	Oct. 4, 9, and 31	Nov. 1
mber of stomachs	50	124	28	28	35
mber empty	15	13	7	0	0
h length (inches)	2.3–5.3	2.3–7.4	3.8–7.5	5.5–7.3	5.8–7.3
pth (fathoms)	2½–7½	4–16	6½–8	3½–11	26
ustacea	86 (25)	57 (14)	19 (4)	95 (37)	100 (100)
Copepoda					
Diaptomus	–	8 (tr)	7 (tr)	17 (tr)	–
Cyclopidae	20 (tr)	–	–	–	–
Cladocera					
Daphnia	52 (25)	22 (11)	4 (tr)	92 (34)	–
Alona	12 (tr)	–	–	17 (2)	–
Unidentified	–	13	6	–	–
Ostracoda	–	15 (tr)	–	8 (1)	–
Mysidacea					
Mysis	–	–	–	–	100 (100)
Amphipoda	–	6	–	–	–
Pontoporeia	–	4 (tr)	4 (4)	–	3 (tr)
Gammarus	–	4 (tr)	–	–	–
Achnoidea					
Hydracarina	–	2.4 (tr)	–	–	–
ecta	8 (50)	71 (59)	58 (46)	17 (63)	–
Ephemeroptera					
Hexagenia	2 (42)	14 (25)	45 (40)	17 (63)	–
Ephemera	2 (4)	2 (6)	4 (3)	–	–
Diptera					
Tendipedidae	4 (4)	51 (8)	–	–	–
Unidentified	–	2 (tr)	9 (3)	–	–
Remains	4 (tr)	7 19	–	–	–
h	8 (25)	7 (27)	23 (49)	–	2 (tr)
Smelt (young)	–	–	23 (49)	–	–
Notropis spp.	8 (25)	6 (27)	–	–	–
Remains	–	2 (tr)	–	–	2 (tr)
bris	–	–	–	–	8 (tr)

me, 14 percent) and relatively unimportant September (frequency, 19 percent; volume, percent). The significance of the domiance of crustaceans in the November 1 sample is questionable since these fish were caught such deep water that their stomach contents may not be compared with those of fish ught at lesser depths in other months.

Cladocerans made up the bulk of the crustaans, except in November when the smelt of e deep-water sample had eaten *Mysis* almost exclusively. *Daphnia* was far more imortant than *Alona* which was consumed in nall amounts and only in July and October. Copepods were eaten in every month but November, ostracods in 2 months, and amphipods in 3 months, but at no time did the rate of occurrence exceed 20 percent (copepods in July) or the percentage volume 3 percent (amphipods in September).

Insects made up at least half the food volume in 3 of the 4 months in which foods other than Crustacea were eaten and in the fourth month (September) accounted for 46 percent of the total. The percentage frequency ranged widely from only 8 percent in July (volume, 50 percent) to 71 percent in August.

The mayfly genus *Hexagenia* strongly dom-

TABLE 4.—*Percentage frequency of occurrence and percentage of total food volume for major food categories of Saginaw Bay smelt, age-group I and older, 1956*

Item	Percentage value for month					
	July	August	September	October	November	Average[1]
Crustacea						
Percentage occurrence	86	57	19	95	100	71
Percentage volume	25	14	4	37	100[2]	36
Insecta						
Percentage occurrence	8	71	58	17	0	31
Percentage volume	50	59	46	63	0	44
Fish						
Percentage occurrence	8	7	23	–	2	8
Percentage volume	25	27	49	–	0[3]	20

[1] Unweighted.
[2] More than 99.5.
[3] Less than 0.5.

inated the insect food of the Saginaw Bay smelt during the 4 months insects were found in stomachs. This form regularly made up the bulk of the identifiable insect material and in individual months contributed 25 to 63 percent of the total food volume. The percentage representation varied from 2 percent in July, when the contribution to the total diet was 42 percent, to as high as 45 in September, when *Hexagenia* contributed 40 percent of the total food. The mayfly *Ephemera* was taken in 3 months, but the contribution to the total food volume did not exceed 6 percent. Dipterans were consumed only in July and August. In the latter months they were present in 51 percent of the stomachs but made up only 8 percent of the total food volume.

Consumption of fish by smelt was confined almost entirely to the 3-month period, July–September. The percentages of total volume in these months were 25, 27, and 49, and the percentages of stomachs containing fish were 8, 7, and 23. All identifiable fish belonged to the minnow genus *Notropis* in July and August, and all were young smelt in September. No stomach contained any commercially exploited species other than smelt. The incidence of fish in the stomachs was greater among large than among small smelt.

The observations on the food of Saginaw Bay smelt agree with the findings of Schneberger (1937) on the smelt of Green Bay, Lake Michigan, in that the smelt of both areas subsisted mainly on invertebrates and consumed more of their own species than of any other kind of fish. The two series of samples did, however, show considerable difference of detail. In Green Bay the most important food item, by a wide margin, was *Mysis*, found only in the deep-water collection of November 1 from Saginaw Bay. On the other hand, *Hexagenia*, a form of major importance in Saginaw Bay, had been consumed by few smelt in Green Bay. Fish other than smelt eaten in Green Bay were *Cottus* and the burbot, *Lota lota*. Most of the differences between the diets of smelt in the two areas probably can be attributed to differences in the availability of food items at the time, place, and depth of collection. Available evidence indicates that the smelt is a versatile feeder.

SMELT AS A COMPETITOR AND PREDATOR

The almost total dependence of young-of-the-year smelt of Saginaw Bay on crustaceans and the predominance of insects and crustaceans in the diet of older fish show that the species is a competitor of the young of all associated species and of the older individuals of many. Detailed appraisal of the smelt as a competitor for food in Saginaw Bay is not possible because there is insufficient information on the food habits of the various fishes. Published records are available only for yellow perch (Tharratt, 1959). The comparison of Tharratt's records with those of the present study reveals that perch and smelt do consume many food items in common. A similar situation probably holds for other species.

Adverse effects of food competition by smelt on other species depend on a rate of consumption so great that a food scarcity develops. The heavy runs of smelt in tributary streams and the experimental fishing by the research vessel *Cisco*[3] indicate that the population is large, but there is no evidence of adverse effects on other species. El-Zarka (1959) pointed out that the assumption of a food scarcity for Saginaw Bay perch in recent years was not tenable since fish collected in 1943–55 averaged heavier, length for length, than did perch collected in 1929–30 (before smelt became plentiful in the bay).

The present study, like the earlier (1937) investigation by Schneberger in Green Bay, failed to indict the smelt as a significant predator on commercially exploited species, except possibly the smelt itself.

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Exchange of Zinc with Environmental Solutions by the Brown Bullhead

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ABSTRACT

Juvenile brown bullheads (*Ictalurus nebulosus*) exposed to dilute solutions of zinc chloride tagged with $zinc^{65}$ showed an initially rapid uptake of zinc for the first several hours followed by a short period of decline. After about 12 hours the accumulation of zinc proceeded at a reduced rate. The highest concentrations in the tissues were found in viscera and gills, with lower amounts in the skin, muscle, and bone. Swallowed water does not contribute appreciably to the zinc in the gastro-intestinal tract. Nearly half of the zinc accumulated after prolonged immersion in a 6-p.p.m. solution was lost during the first day after transfer of the fish to flowing, fresh water, and only slightly more after 7 days. There was no apparent damage to the fish from exposure to zinc concentrations as high as 12 p.p.m. for 14 days, nor from the effects of the radiation from the $zinc^{65}$ in the solutions.

INTRODUCTION

The bivalent metals of the transition elements have a strong tendency to complex with many organic functional groups such as those associated with serum proteins (iron in haeme, copper in haemocyanin) and metallo-enzymes (zinc in carbonic anhydrase). Harvey (1955) proposes one or more of three mechanisms for the concentration of trace metals by marine organisms. They are: adsorption of ions on cell-water interfaces or at interfaces within the cell; absorption from solution in the sea by passage through semi-permeable membranes into the body fluids and subsequent concentration in specific tissues; and the attachment to the mucus surrounding aquatic plants and animals of colloidal micelles of hydrated oxides of iron and manganese or colloidal alumina or silica to which metallic ions are adsorbed.

The presence of trace amounts of zinc in fish has been well established since Bodansky (1920, 1922) determined it in 14 species. Evidence of the presence of the radioisotope $zinc^{65}$ in fish samples from the Pacific Ocean following nuclear test explosions has been reported by Seymour *et al.* (1957), Lowman, Palumbo and South (1957), and Welander (1957). Chipman, Rice, and Price (1958) studied the uptake, accumulation, and loss of the radionuclide $zinc^{65}$ in marine plankton, fish, and shellfish. Their experiments with Atlantic croakers (*Micropogon undulatus*) and pinfish (*Lagodon rhomboides*) showed a rapid uptake from the digestive tract by the visceral organs and a rapid loss of $zinc^{65}$ accumulated from solution when the fish were returned to flowing sea water. The bone, integument, and muscle appeared to be sites o accumulation of the radionuclide.

The accumulation of zinc ions in fish live cells against a sevenfold concentration gradi ent was considered by Saltman and Borough (1960) to be a passive mechanism, not di rectly coupled to metabolic energy, in which zinc was sorbed to specific binding sites o or within the cells.

Chaberek and Martell (1959, p. 451) cit the outer surface of vertebrate bone as an ion exchange medium capable of adsorbing larg quantities of metal ions. A foreign metal ma be transported to the bone as a serum protei complex and there exchange with bone C (II) or Mg(II).

In this experiment the uptake of zinc b brown bullheads (*Ictalurus nebulosus*) fro different environmental concentrations wa examined.

MATERIALS AND METHODS

The *Ictalurus nebulosus* specimens used i this experiment were captured from swarm of juveniles in Lake Washington, Seattle Washington. Groups of three fish, weighin approximately 8 grams per group, were im mersed in 2-liter volumes of lake water con taining 0.25, 0.50, 1.00, 3.00, 6.00, and 12.0 p.p.m. of zinc as chloride. The zinc in the firs five of these preparations was tagged with th radioisotope $zinc^{65}$. Table 1 shows the weigh of each group of fish, the concentration o zinc, and the amount of radioisotope in thes preparations. Five-liter pyrex aquaria wer used.

The uptake of zinc was determined b counting the radiation in each group of fis at intervals after their exposure to the radio

ABLE 1.—*Weight of fish, concentrations of zinc, and amount of radioisotope in experimental solutions*

Item	Group				
	I	II	III	IV	V
eight of fish (grams)	8.1	8.2	8.0	7.7	8.1
in water (p.p.m.)	0.25	0.5	1.0	3.0	6.0
^{65} in water (μc)	10.3	10.3	10.3	30.8	61.6

itive solutions. On the assumption that the diozinc was uniformly distributed with respect to the stable isotopes in the solutions, e amount of zinc taken up by the fish was lculated as a function of the radioactivity.

The radioactivity was measured with a mma-ray scintillation spectrometer with a by 3-inch diameter, thallium-activated, sodium iodide crystal. To eliminate counting rors due to interference with low energy, attered Compton rays by the body of the sh and container materials, only that portion the gamma spectrum between 1.04 and 1.20 ev, containing the principal zinc^{65} photoak at 1.12 Mev was utilized.

After exposure to the zinc solution, each oup of fish was removed from the aquarm, rinsed in distilled water, and placed oist in a polyethylene container in the specometer for determination of the radiation. he counting time for each group was 5 mines and the range of total counts from 735 45 to 10, 990 ± 120 (0.9 error). Correcons were made for radioactive decay, background radiation, and changes in the sensitivy of the spectrometer.

After 96 hours' total exposure time, all the sh from the radioactively tagged solutions, xcept those from the 6.0-p.p.m. solution, were issected. Gastrointestinal tract, kidney, gills, ver, spleen, skin, muscle, and bone tissues om each of these fish were pooled and dried. he dried tissues were analyzed for radioacvity due to zinc^{65}. Loss of accumulated zinc as determined by placing fish, which had een exposed to the 6-p.p.m. solution of zinc r 96 hours, into a hatchery basket immersed n flowing lake water and determining the esidual radiation at daily intervals for 7 ays.

The water in all experimental solutions was rom the University of Washington hatchery. n analysis of this water by the Washington tate Game Department is shown in Table 2. n x-ray spectrographic analysis of this wa-r with a sensitivity to 0.01 p.p.m. failed to eveal a measurable amount of zinc.

TABLE 2.—*Chemical analysis of lake water from the University of Washington hatchery, 1956*[1]

[Quantities expressed as parts per million]

Item	Concentration
Total solids	102
pH	7.6
Loss on ignition	10
Fixed residue	92
Total hardness (as $CaCO_3$)	73.8
Calcium hardness (as $CaCO_3$)	25.3
Magnesium hardness (as $CaCO_3$)	47.5
Alkalinity (as $CaCO_3$)	32
Acidity (as $CaCO_3$)	1.55
Phosphorus	0
Sulfate	16.5
Chloride	9.8
Silica (as SiO_2)	11.5
NH_4 nitrogen	trace
Total nitrogen	0.3
NO_2 nitrogen	trace

[1] Analysis by Washington State Game Department.

RESULTS

Gross uptake of zinc

The uptake of zinc by the fish from five different concentrations of zinc in water for exposure intervals up to 96 hours is shown in Table 3. Figure 1 shows the zinc uptake in micrograms of zinc per gram wet weight of fish plotted against time of exposure to concentrations in water of 0.5, 3.0, and 6.0 p.p.m. of zinc. The curves reveal a characteristically rapid initial uptake of zinc, followed by a decrease within the first few hours after exposure, then a resumption of the accumulation of zinc, but after about 12 hours at a lower rate than initially exhibited.

Accumulation of zinc in specific tissues

The accumulation of zinc in pooled samples of eight different tissues dissected from the fish which had been exposed for 96 hours

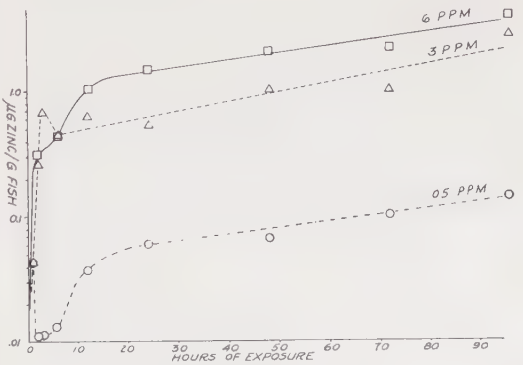

FIGURE 1.—The uptake of zinc from water by groups of brown bullheads exposed to three different concentrations.

TABLE 3.—*Uptake of zinc from water by the brown bullhead*

[Expressed as micrograms of zinc taken up per gram of fish]

Exposure time (hours)	Group (and p.p.m. Zn in water)				
	I (0.25)	II (0.5)	III (1.0)	IV (3.0)	V (6.0)
1	0.012	0.043	0.050	0.045	0.176
2	0.0	0.011	0.022	0.267	0.320
3	0.010	0.011	0.027	0.686	0.338
6	0.003	0.013	0.008	0.462	0.432
12	0.024	0.039	0.080	0.638	1.050
24	0.045	0.061	0.025	0.529	1.510
48	0.066	0.067	0.100	1.040	2.110
72	0.121	0.102	0.150	1.030	2.210
96	0.149	0.143	0.215	2.950	3.960

to radioactive solutions, expressed in relative values derived from their radioactivity, is shown in Table 4. The gastrointestinal tract, kidney, gills, liver, and spleen concentrated the most zinc; the bone, muscle, and skin the least.

The gastrointestinal tract accumulated more zinc by weight than any of the other tissues tested. The fish were starved during the experiment and although there was little likelihood of much water entering the alimentary canal with food, the possibility was considered that swallowed water might have contributed to the high gastrointestinal concentration of zinc, although it is generally acknowledged that fresh-water fish do not swallow water (Smith, 1930).

To test this possibility, a comparison was made of the accumulation of zinc from a 6.00-p.p.m. solution during 48 hours by the tissues of two groups of bullheads. The esophagus of each member of one group was plugged with a mixture of vaseline and beeswax. Each group consisted of one large fish (ca. 140 grams) and three small ones (ca. 8 grams each). Relative values for concentration of zinc in specific tissues are presented in Table 5. From this tabulation it is apparent that the difference in the concentration of zinc in the gastrointestinal tract of each group is negligible and that it is therefore unlikely that swallowed water could be a contributing factor in the accumulation of zinc in these tissues.

TABLE 4.—*Relative concentration of zinc in pooled tissues of brown bullhead exposed for 96 hours to zinc solutions tagged with zinc*^{65}

[Expressed as radioactive counts per minute due to zinc^{65} per gram wet weight of tissue]

Tissue	Dry weight (milligrams)	Counts per minute per gram wet weight of tissue
Gastrointestinal tract	150	3,500
Kidney	53	3,471
Gills	113	2,991
Liver	140	1,614
Spleen	17	1,412
Skin	208	514
Muscle	246	317
Bone	1,091	41

Loss of accumulated zinc

The fish exposed to 6.0 p.p.m. of zinc for 96 hours, when placed in flowing, fresh water, lost 43 percent of their total accumulated zinc after 1 day. The loss therafter was very gradual and by the end of 7 days, only 54.4 percent had been lost (Figure 2). These results are not quite comparable to those obtained by Chipman *et al.* (1958) with the pinfish, which lost most of its accumulated zinc in the first day after immersion in flowing sea water. The swallowing of sea water by marine teleosts to replace the body water lost by osmosis, and the active excretion of excess salts through the gills undoubtedly provide a more efficient system for excess salt disposal than is available to the fresh-water brown bullhead.

Toxicity of zinc to brown bullhead

Bullheads exposed to 12 p.p.m. of zinc for 14 days all survived. Silver, mercury, copper, lead, cadmium, zinc, aluminum, nickel, and chromium have all been classed as metals of relatively high toxicity to fish by Doudoroff and Katz (1953) because metal-protein complexes coagulate on the gill surfaces. Goodman (1951) demonstrated that 6 p.p.m. of

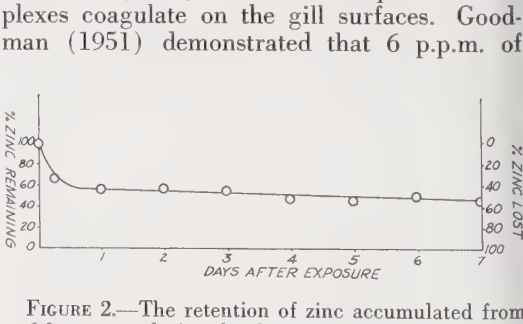

FIGURE 2.—The retention of zinc accumulated from a 6.0-p.p.m. solution by brown bullheads immersed in flowing, fresh water.

TABLE 5.—*The effect of plugging the esophagus on the uptake of radioactively tagged zinc in tissues of the brown bullhead exposed to a 6.0-p.p.m. zinc solution containing zinc*[65]

Tissue	Counts per minute per gram (dry)	
	Control group	Esophagus plugged
Gills	4,708	2,678
Gastrointestinal tract	1,312	1,315
Kidney	701	773
Liver	519	763
Muscle	50	52
Bone	15	56

Zinc in aquarium water was toxic to rainbow trout fingerlings. The bullheads in this experiment may have suffered no apparent ill effects from exposure to 12 p.p.m. because there was calcium in the lake water used to prepare the zinc solution. Jones (1938) found that calcium salts inhibited the coagulation of protein compounds of lead and zinc on the gills. It is also probable that there are differences between taxonomic groups of fish with respect to tolerance to zinc in the water.

There were no observable effects on the bullhead from the radiation from the zinc[65] to which they were subjected during the course of this experiment.

DISCUSSION

A combination of sorption phenomena is believed to account for the features of the gross uptake of zinc from water by bullheads in the experiment described above. These phenomena are: (1) adsorption to mucous substances secreted at surfaces in contact with the external environment; (2) absorption by diffusion of zinc ions across the semi-permeable membranes into the body fluids; (3) adsorption from the body fluids to binding sites on or within specific cells in the body fluids and in internal tissues; and (4) ion-exchange with the Ca(II) and Mg(II) of the apatite of the outer surface of the bone.

TABLE 6.—*Comparison of the amounts of zinc accumulated in bullheads after 12 hours' exposure, with the zinc in volumes of the environmental solutions equivalent to estimated blood volumes of the fish*

Group	Weight (grams)	Blood volume (milliliters)	Zinc in solutions		Zinc in fish
			p.p.m.	μg in blood vol. equivalent	after 12 hrs. (μg)
I	8.1	1.46	0.25	0.37	0.20
II	8.2	1.48	0.5	0.7	0.3
III	8.0	1.44	1.0	1.4	0.6
IV	7.7	1.39	3.0	4.2	4.9
V	8.1	1.46	6.0	8.8	8.5

The rapid initial uptake could then represent a phase in which the first two sorption mechanisms were predominant. The short period of declining accumulation immediately following could be caused by the respiration of the fish increasing the acidity of the environment, returning to solution some of the zinc initially adsorbed to the external surfaces of the fish. The more gradual accumulation of zinc occurring after about 12 hours of exposure could be a phase in which the gradient in the concentration of zinc ions between the external environment and the body fluids was reduced to the extent that absorption of zinc across the semi-permeable membranes proceeded at a rate just sufficient to replace the zinc removed from the body fluids by adsorption and exchange with various tissue components.

If it is assumed that some of the externally adsorbed zinc was removed, in part by the increased acidity of the closed environment from the respiration of the fish, and in part by the distilled water rinse prior to radioactive counting, then much of the zinc accumulated by the fish after about 12 hours of exposure can reasonably be assumed to have been in the blood. Comparison of the amount of zinc in volumes of the environmental solutions equivalent to the computed blood volumes of the fish immersed in them, with the amount of zinc accumulated by the fish after 12 hours of exposure, suggests that by this time the zinc concentration gradient between the external environment and the blood of the fish had been effectively reduced (Table 6). The blood volumes of the fish were estimated by use of a ratio of 0.18 for blood volume in milliliters to body weight in grams from Prosser *et al.* (1950).

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Movement of Native and Hatchery-Reared Game Fish in a Warm-Water Stream[1]

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ABSTRACT

Movement of 248 marked and recaptured native smallmouth bass (*Micropterus dolomieui*), native rock bass (*Ambloplites rupestris*), and hatchery smallmouth bass released in a headwater tributary of the Little Miami River of Ohio during 1953 through 1957 is described. More than 91 percent of the native fishes of both species reported by anglers were taken within ½ mile of release points. Recaptures made with electric shocker and hoop nets indicated that appreciable numbers of native fish remained within limited areas of one to several pools between successive years. Considerable numbers of stocked smallmouth bass moved away from release points. A total of 35.7 percent of fish stocked in optimum habitat in 1953 and later recovered by anglers had moved distances greater than ½ mile. All fish stocked in submarginal habitat upstream in 1955 and later recovered by anglers moved more than ½ mile. Except for one recapture 6 miles upstream from the release point, all returns of stocked fish were from downstream at distances ranging up to 70 miles. The proportion of fish stocked in optimum habitat in 1953 and recaptured 11 to 50 miles downstream increased significantly from 1953 to 1954, suggesting a progressive downstream dispersal. Movement of hatchery smallmouth bass was independent of size at stocking in 1953. Rapid disappearance of the 1953-stocked fish may have resulted from higher mortality, as well as from movement.

INTRODUCTION

Information about movement of warm-water fish is useful in many biological and fish-management studies. The present report describes data from 248 recaptures from 2,270 game fish tagged and released in Massie Creek, a small headwater tributary of the Little Miami River in southwestern Ohio. Six hundred thirty-seven native smallmouth bass (*Micropterus dolomieui*), 740 native rock bass (*Ambloplites rupestris*), and 893 hatchery-reared smallmouth bass were tagged (Table 1). Native fish were tagged in conjunction with studies of distribution, age and growth, reproduction, and harvest by anglers. Two groups of hatchery smallmouth bass were tagged and released to test success of stocking in an area with a sizable native population and in a submarginal area where the species apparently had become extirpated. Tagged fish were recovered by anglers and with electric shocker and hoop nets.

A substantial amount of information on movement of native centrarchid fish in streams has been gathered during recent years. Scott (1949) found that rock bass tended to remain within very limited areas of an Indiana stream. Gerking (1950) recorded a high degree of areal stability for sunfish (*Lepomis* spp.) and rock bass collected before and after a flash flood in Richland Creek, Indiana. Larimore (1952), after displacing smallmouth bass from points of capture in an Illinois stream, observed "homing" responses by many of the displaced fish. Gerking (1953) found over a 4-year period that longear sunfish (*Lepomis megalotis*) and rock bass had strong tendencies to remain within 100- to 200-foot sections of a bedrock stream between successive years while smallmouth bass tended to remain within stream sections of about twice that length. To describe such behavior, he used the classical concepts of home range and territory. Funk (1957) analyzed movement of stream fish on the basis of statewide tag returns by Missouri anglers. He described the smallmouth bass and rock bass as "sedentary" but believed there were sub-groupings of mobile fish that accounted for small percentages of longer movements. Experiments by Gunning (1959) have shown that the olfactory mechanism appears to control homing by the longear sunfish. Recently, Gerking (1959) has reviewed the literature on restricted movement of many fresh-water and marine fishes.

Movement of stocked centrarchids in streams has received less attention. Wickliff (1933) reported on a small number of fish trap-netted from Lake Erie and recaptured after being released in different Ohio streams. The most comprehensive study was by Larimore (1954) who observed stocked smallmouth

[1] Contribution from Dingell–Johnson Project F-1-R, Ohio.

bass in relation to a resident population in Jordan Creek, Illinois.

THE STUDY STREAM

Massie Creek flows southwesterly through Clark and Greene Counties for 22 miles and joins the Little Miami River 4½ miles north of Xenia. Its width and maximum depth at 40 survey pools along the lower 8½-mile section averaged 38 and 2.6 feet, respectively, during low flow in the summer of 1956; and the mean daily discharge 4 miles above the mouth from October 1, 1952, to September 30, 1957, was 38 cubic feet per second. A steep gorge carved in dolomite and limestone at Cedarville divides the creek into two distinct areas: one which flows through open farmland with gradients less than 10 feet per mile; and a second downstream which flows through wooded pastures in a rock and rubble stream bed with a gradient of approximately 18 feet per mile. A mill dam in the gorge 8½ miles from the mouth isolates fish in the headwaters from populations downstream.

TAGGING PROCEDURES

Fish were tagged by placing butt-end jaw tags, similar to bird leg bands, around the right mandible.[2] The open tag was closed around the lower jawbone so that in most cases enough space remained for considerable growth of the mandible. Tag retention was not tested, but other investigators have shown, particularly with trout, that the band-type tag on the mandible is among the most permanent marking methods (Corson, 1957; Mullan, 1958). Fish tagged in the present study were recaptured after being at large approximately 3 years or less.

All native smallmouth bass tagged came from the 8½ miles of creek downstream from the Cedarville gorge, an area which contained the highest populations of smallmouth bass and total fishes within the Little Miami River headwater area (Brown, 1960). Bass were not taken from the area above the gorge with a shocker, hoop nets, and seines, or by the creel census. Native smallmouth bass tagged in 1953 and 1954 were caught with hook and line by fishery technicians. Those tagged in 1955, 1956, and 1957 were caught in summer with an electric shocker from 40 survey pools.

[2] Style 4F-1242M-Monel, sizes 6, 8, 10, and 12, manufactured by the National Band and Tag Company, Newport, Kentucky.

Native rock bass, which were more generally distributed than smallmouth bass, were captured from both the upper and lower areas of Massie Creek. They were taken in the lower section along with smallmouth bass and in addition by shocker from the upper area during the summer of 1955 and by hoop nets from both areas during spring, fall, and winter months of 1953–55.

Marked hatchery smallmouth bass were released in the lower area on March 11–12, 1953, and in the upper area on October 18, 1955. All hatchery fish were distributed approximately ⅛ mile above and below bridges which span the creek at fairly regular intervals. Five hundred ninety-nine age-group-I bass from the Xenia hachery were released in 1953, and 294 age-group-O bass from the Newton hatchery were released in 1955. Since efforts were made to tag larger individuals, the stocked fish did not represent random samples from the hatcheries. Physical condition of the fish appeared to be excellent at both releases, and handling mortality was not observed at anytime during the immediate post-stocking periods.

NATIVE SMALLMOUTH BASS

Tags from 70 native smallmouth bass were returned by anglers during the 1953–59 period, representing 11.0 percent of the native fish marked from 1953 through 1957. Returns ranged from 6.4 percent of the comparatively large number tagged in 1957 to 25.0 percent of the small number tagged in 1954 (Table 1). Catches of many other tagged fish probably went unreported despite signs posted along the stream and frequent presence of fishery workers in the area. In addition to fish caught by anglers, 34 tagged native smallmouth were recaptured with an electric shocker during the summers of 1956 and 1957. The latter returns are considered separately because of areal bias associated with the collection procedure.

Sixty-four fish, representing 91.4 percent of the tagged native smallmouth bass reported by anglers, were recaptured within ½ mile or less of release points. Fifteen fish, representing 21.4 percent of anglers' returns, were recaptured within less than ⅛ mile of release points, and 15 fish (21.4 percent) moved from ⅛ to 19 miles. Capture sites of 40 fish (57.1 percent) could not be accurately determined from information furnished by anglers, but these fish may have moved from 0 to approximately

ABLE 1.—*Length–frequency distribution of native and hatchery-reared game fish tagged and released in Massie Creek during the period 1953 through 1957*

[Numbers of fish released upstream from Cedarville are in parentheses]

otal length (inches)	Native smallmouth bass[1]					Native rock bass										Hatchery smallmouth bass	
	1953	1954	1955	1956	1957	1953		1954		1955		1956		1957		1953	1955
3.0– 3.9	–	–	–	–	–	–	–	–	–	–	(3)	–	–	–	–	24	–
4.0– 4.9	1	–	–	2	–	2	(13)	14	(6)	12	(12)	20	–	4	–	353	–
5.0– 5.9	3	4	7	34	3	14	(8)	38	(6)	34	(28)	91	(1)	52	–	117	(17)
6.0– 6.9	21	3	14	34	36	15	(7)	10	(1)	52	(31)	60	(1)	65	(1)	54	(82)
7.0– 7.9	25	2	14	37	63	8	(9)	3	(3)	16	(10)	37	–	20	–	24	(140)
8.0– 8.9	26	4	12	26	76	10	(1)	1	–	2	(3)	4	(2)	6	–	25	(55)
9.0– 9.9	17	2	18	13	26	1	–	–	–	1	(1)	–	–	–	–	2	–
0.0–10.9	7	4	13	12	11	–	–	–	–	–	(1)	–	–	–	–	–	–
1.0–11.9	6	5	1	11	3	–	–	–	–	–	–	–	–	–	–	–	–
2.0–12.9	4	3	4	6	4	–	–	–	–	–	–	–	–	–	–	–	–
3.0–13.9	1	1	1	3	6	–	–	–	–	–	–	–	–	–	–	–	–
4.0–14.9	1	–	1	1	3	–	–	–	–	–	–	–	–	–	–	–	–
5.0–15.9	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
otal marked	112	28	85	179	233	50	(38)	66	(16)	117	(89)	212	(4)	147	(1)	599	(294)
eturns[2]	20	7	14	14	15	6	(3)	3	–	2	(1)	8	–	3	(1)	57	(13)
rcentage return	17.9	25.0	16.5	7.8	6.4	12.0	7.9	4.5	–	1.7	1.1	3.8	–	2.0	100.0	9.5	4.4

[1] Native smallmouth bass of 1953 and 1954 were measured only to the nearest ¼ inch, making their placement in gth groups approximate.
[2] Numbers of returns from all years for fish tagged in given years.

½ mile. Recaptures in succeeding years after release on the basis of all calendar years combined is shown in Table 2. The proportions of recaptures exhibiting movement (⅛ mile or more) increased in proportion to number of years at large, although the small number of returns does not conclusively define such relationship.

Distances and directions traveled by native smallmouth bass (including three fish recaptured by electric shocker) which traveled from ⅛ to 19 miles and whose exact location of catch is known are listed in Table 3. Ten fish moved upstream and 8 down, but the three longest moves of 5½, 6, and 19 miles were downstream. The maximum possible upstream distance was limited by the Cedarville mill dam to about 8½ miles. Some of the movements may have been associated with spawning activity, although the data are not extensive enough to evaluate individual factors. Smallmouth bass nested as early as April 13 and remained at nest sites as late as the end of June during 1953–57, and many of the tagging and recapture dates fell near or within the spawning season. A fish tagged or recaptured in spring may have been moving toward, nesting at, or returning from a spawning site.

Electrofishing in 1956 and 1957 showed that at least a fraction of the native smallmouth bass population remained within extremely limited areas during 1-year periods. Twenty-two of 35 recaptured fish tagged in 1955 and 1956 were retaken from either the same or the immediately adjacent upstream or downstream pools, 10 fish were recaptured from three-pool areas in which individual pools were not identified, and 3 fish moved distances from ⅛ to 1 mile. These data are

ABLE 2.—*Comparison of the number of years at large and relative mobility of native smallmouth bass of Massie Creek, based on recaptures by anglers for all years of the period 1953–59*

Year of recapture	Number of tagged fish caught						Total
	0–½ mile		< ⅛ mile		⅛–19 miles		
	Number	Percentage	Number	Percentage	Number	Percentage	
st[1]	18	60.0	10	33.3	2	6.7	30
2nd	20	60.6	4	12.1	9	27.3	33
3rd	2	33.3	1	16.7	3	50.0	6
4th	—	—	—	—	1	100.0	1
Total	40	—	15	—	15	—	70

[1] Within the same calendar year as tagged.

TABLE 3.—*Distances and directions traveled by 18 native smallmouth bass whose exact location of capture by anglers and electric shocker during 1953–58 is known*

Date		Time at large (months)	Total length when tagged (inches)	Miles traveled	
Tagged	Recaptured			Upstream	Downstream
1953					
April	July 1953	3	7¾	—	5½
May	July 1954	14	10	½	—
July	July 1954	12	7¾	½	—
October	April 1954	7	8	½	—
April	June 1953	26	8½	—	6
May	April 1955	23	12½	½	—
August	April 1956	33	8¼	1	—
1955					
August	September 1955	2	12	—	19
August	October 1956	14	5½	⅛	—
August	August 1956[1]	12	6½	—	1
August	June 1956	10	8	—	½
July	August 1957[1]	25	9	⅛	—
1956					
June	July 1957[2]	13	7½	—	⅛
June	May 1957[2]	11	6½	—	⅛
June	July 1957	13	9¼	—	⅛
August	August 1957[1]	12	7¼	1	—
August	September 1957	13	7½	2¼	—
July	May 1958	22	13¼	3½	—

[1] Recaptured by electric shocker.
[2] Previously recaptured at areas of release in the fall of 1956.

somewhat biased, however, in favor of less mobile fish because annual population work was concentrated at 40 permanent survey pools distributed along the creek in several-pool clusters. Alternate areas where tagged fish might have moved went unchecked.

NATIVE ROCK BASS

Twenty-seven marked native rock bass or 3.6 percent of those tagged in 1953–57 were returned by anglers during the 1953–59 period. Percentage return ranged from 1.4 percent for 206 fish tagged in 1955 to 10.2 percent for 28 fish tagged in 1953 (Table 1). In addition to fish caught by anglers, 22 native rock bass were recaptured in hoop nets during spring, fall, and winter months of the period 1953 through 1955, and 25 were recaptured by electric shocker during the summers of 1955, 1956, and 1957. Twenty-one (91.3 percent) of 23 fish reported by anglers were recaptured within ½ mile or less of release points. Eleven fish (47.8 percent) were recaptured within less than ⅛ mile, and five (27.7 percent) moved from ¼ to 3½ miles. Exact capture sites of the remaining seven fish (47.8 percent) could not be determined, but they moved less than ½ mile if at all. The small number of returns did not warrant conclusions on time and movement relationships.

Data on distances and directions traveled by native rock bass including fish recaptured by electrofishing and hoop-netting are shown in Table 4. Eight out of 10 movements were upstream. One fish caught by hoop net on October 1, 1953, was recaptured by hook and line on May 1, 1954, at the foot of a low dam ½ mile upstream, and on October 29, 1954, it was recaptured by hoop net downstream where it had first been caught and tagged. Another fish tagged on April 6, 1955, was recaptured 13 days later 3½ miles upstream. The greater tendency to move in spring may have been associated with spawning since either tagging dates, recapture dates, or both fell during or near the spawning period (Table 4). Rock bass nests in Massie Creek began to appear a week or two later than the first smallmouth bass nests, and rock bass were spawning heavily in mid-June when spawning of smallmouth bass had neared an end.

The sedentary character of at least a fraction of the native rock bass populations was evident from fish recaptured in hoop nets and by electrofishing. Nineteen fish were renetted from the same pools during the first calendar years after tagging. Fourteen fish were retaken by electrofishing from within two- to four-pool segments during the first years after tagging, and two other fish were retaken from the same pools during the second and third years, respectively, after tagging. Five additional fish recaught during electrofishing and hoop-netting may or may not have moved within ½-mile segments. The few positive movements are cited in Table 4. Exactly what

TABLE 4.—*Distances and directions traveled by native rock bass of Massie Creek taken by anglers, electric shocker, and hoop net during 1953 through 1957*

Date		Time at large (months)	Total length when tagged (inches)	Miles traveled	
Tagged	Recaptured			Upstream	Downstream
1953					
October	May 1954	7	6	½	—
October	October 1954[1]	6	6¼	—	½
April	July 1955[2]	27	6½	½	—
September	April 1955	19	5¾	½	—
1954					
October	June 1956[2]	20	5¼	¾	—
October	April 1956	18	5¾	¼	—
1955					
April	July 1956[2]	15	6	—	1½
July	June 1956	11	8¾	1¼	—
April	April 1955	12	7	3½	—
1956					
July	August 1957[2]	13	5½	½	—

[1] Recaptured by hoop net, representing the second recapture for the preceding fish taken by an angler on May 1, 1954.
[2] Recaptured by electric shocker.

portion of the population the sedentary fish represented is not known since the collections were from widely separated sampling sites.

HATCHERY-REARED SMALLMOUTH BASS

Tags from 57 (9.5 percent) of the smallmouth bass stocked on March 11–12, 1953, in Massie Creek below Cedarville were returned by anglers during the 1953–55 period. Tags from 13 (4.4 percent) of the fish stocked on October 18, 1955, in the upper area were returned during 1956 and 1957 (Table 1). Stocked fish were not taken by the electric shocker. A lapse of 2 years occurred between the 1953 stocking and the start of electrofishing during the summer of 1955 in 4.5 acres of Massie Creek below Cedarville dam. In 1956 and 1957, 40 pools totaling 8.5 acres or 28 percent of the estimated total pool area below Cedarville dam were sampled. If tag returns by anglers were proportional to the 1953-stocked fish present in and below the stream each year (Table 5), there were few chances of taking any by shocker. The area above Cedarville was not checked by shocker after the 1955 stocking, but a single return was made there by hoop net on October 27, 1955, 1½ miles below the release point.

In marked contrast to native fishes, considerable numbers of stocked smallmouth bass moved away from release points. Twenty-one fish, representing 35.7 percent of the 1953-stocked bass reported by anglers, moved distances greater than ½ mile compared to less than 9 percent for both species of native fish. All but one of the recorded movements from the 1953 stocking were downstream. The 13 recaptures by anglers of the 1955 stocking also were taken downstream at distances greater than ½ mile. The only fish from the 1953 releases which moved upstream covered 6 miles, while the downstream distances ranged up to 70 miles traveled by a fish taken near a lock in the Ohio River at Cincinnati.

A comparison of time at large and distance traveled (Table 6) indicates the rather rapid and seemingly progressive downstream movements of the stocked smallmouth bass recaptured by anglers. One fish of the 1953 release moved at least 6 miles before the end of March, a second at least 21 miles before the end of May, and a third at least 41 miles by the end of September. Two fish of the 1955 release moved at least 31 miles by May of 1956. The ratio of fish recaptured from the 1953 release that moved 0–10 and 11–50 miles decreased greatly in 1954, tending to emphasize the downstream dispersal. A test of independence applied to the following data

TABLE 5.—*Estimated numbers of smallmouth bass from the stocking of March 11–12, 1953, that were present in and below Massie Creek in subsequent years*

[Computed by direct proportion from tag returns by anglers]

Year	Age group	Number of tag returns by anglers	Estimated number of tagged fish present
1953	I	47	599[1]
1954	II	9	114
1955	III	1	13
1956	IV	0	—
1957	V	0	—

[1] Total number of fish stocked.

TABLE 6.—*Comparison between time at large and miles traveled by hatchery-reared smallmouth bass stocked in Massie Creek on March 11–12, 1953, and October 18, 1955, and recaptured by anglers during 1953 and 1956, respectively*

Year and month of recapture	Miles traveled									Total number of fish
	<⅛	0–½	⅛–½	1–5	6–10	11–20	21–30	31–40	41–50	
1953										
March	1	–	–	–	1	–	–	–	–	2
April	7	2	3	–	–	–	–	–	–	12
May	7	4	1	–	1[1]	1	1	–	–	15
June	–	–	–	–	–	–	2	–	–	2
July	2	1	–	–	–	–	–	–	–	3
August	1	–	–	1	1	–	–	–	–	3
September	4	–	–	–	–	–	–	–	1	5
October	1	–	–	–	–	–	–	2	–	3
Total	23	7	4	1	3	1	3	2	1	45
1956										
May	–	–	–	4[2]	–	–	–	2	–	6
June	–	–	–	2	–	–	–	–	–	2
July	–	–	–	–	–	1	–	–	–	1
September	–	–	–	–	–	1	–	–	–	1
Total	–	–	–	6	–	2	–	2	–	10

[1] This fish moved upstream for the only upstream movement recorded.
[2] One of these fish was taken in a hoop net on October 27, 1955, 1½ miles below the release point; on May 5, 1956, it was caught by an angler 2¾ miles farther downstream, as recorded here.

gave a chi-square value of 10.96 which indicates a highly significant difference between the ratios (Snedecor, 1956):

Year	Number of recaptures (0–10 miles)	(11–50 miles)	Ratio
1953	38	8	4.75
1954	2	7	0.28

Because there was a maximum length difference of almost 6 inches between individual fish of the 1953 stocking, the influence of size at stocking upon the rate of recapture by anglers in 1953 was examined. There was a pronounced difference between the number of fish in the 4.0–4.4- and 4.5–4.9-inch size classes of the original planting and the relative number in these classes of the anglers' returns in 1953. Although representing 33.5 percent of the total stocked fish, the 4.0–4.4-inch length group contributed only 9.5 percent to the 1953 recaptures. The data of Table 7 show that with exclusion of fish smaller than 4.5 inches there was no significant variation from a random return of tagged fish in respect to the original length-frequency distribution. Returns in 1956 of the more homogeneous 1955 release in the upper area also were random in respect to original lengths; chi square equaled 0.87 with 1 degree of freedom.

To test whether size at stocking influenced movement, tag returns by anglers from fish above 4.4 inches were arbitrarily arranged in the length groups and distance intervals shown in Table 8. None of the resulting chi squares approached the 5-percent level of significance which would have led to rejection of the hypothesis that movement was independent of fish size.

MANAGEMENT IMPLICATIONS

Under headwater conditions as observed at Massie Creek it is apparent that native smallmouth bass and rock bass are characterized by a fairly high degree of areal stability. This finding is in general agreement with the work cited previously and, more specifically, with a conclusion drawn by Gerking (1953): ". . . it appears that the fish population of a small stream may be thought of as a series of discrete natural units rather than as a single, homogeneous, freely-mixing group." Chances of intermixing over distances of 5 or 10 miles appear to be small for the majority of fish produced in a local area and should not repre-

TABLE 7.—*Test for the influence of size at stocking upon the return of smallmouth bass by anglers in 1953*

[Expected returns computed from the release totals of 225, 323, and 51 fish of the respective length groups are in parentheses]

Test status of the 3.5–4.4-inch length group	Number of fish reported by original length groups in inches			Degrees of freedom	Chi square
	3.5–4.4	4.5–6.9	7.0–9.4		
Included	4(15.8)	32(22.6)	6(3.6)	2	14.32*
Excluded	–	32(32.8)	6(5.2)	1	0.17

*Significant at the 1-percent level.

TABLE 8.—*Tests of independence between lengths of smallmouth bass at stocking on March 11–12, 1953, and miles traveled, returns of 1953, 1954, and 1955 combined*

Total length (inches)	Number stocked	Number of fish reported by miles traveled		Degrees of freedom	Computed chi square[1]
		0–10	11–70		
5–6.9	323	26	12	1	0.224
0–9.4	51	6	1		
5–5.4	228	18	11	1	2.13
5–9.4	146	14	2		
5–5.4	228	18	11	2	3.28
–7.4	110	9	1		
5–9.4	36	5	1		

[1] At the 5-percent level of significance, chi square equals 84 with 1 degree of freedom and 5.99 with 2 degrees of edom.

nt a limitation in age-growth work or other mparative analyses where adequate samples re available.

In comparison with the relative stability of ative fish, the prominent downstream move- ent of considerable numbers of hatchery- ared smallmouth bass from areas of opti- um habitat in Massie Creek represents a mitation of stocking as a practicable manage- ent tool.

The phenomenon of high mobility for ocked bass was recorded by Wickliff as early s 1933. He described 10 returns from 717 mallmouth bass and 15 returns from 533 ock bass that had been trap-netted in Lake rie and released in Ohio streams. Long ownstream movements were noted for both pecies including one of 204 miles in less than months for a smallmouth bass released in he Stillwater River above Dayton. Limited eturns resulting from distribution of the fish hroughout the State and from use of oper- ular tags, now known to be extremely im- ermanent, made the findings exploratory at est.

More recently, Larimore (1954) observed that 76 percent of the pond-reared smallmouth bass planted and recaptured in Jordan Creek, Illinois, moved upstream or remained in the area of planting. Only four fish were found more than 0.4 mile below the stocking place. He also showed that increase in yield to anglers was approximately equal to stocked fish which were retaken (33 percent of plant).

A similar upstream dispersal was not observed following the 1953 Massie Creek stocking, although as in the Jordan Creek study, a portion of the stocked fish apparently became adapted to conditions within ½ mile of release points. Comparison between the two studies indicates there is some uncertainty about the great reduction in returns from within 10 miles of release points along Massie Creek in 1954 in contrast to increased returns by anglers from far downstream. Finally it can be questioned whether some fish among the Jordan Creek releases might also have moved long distances from the 4-mile experimental segment where identification by anglers would not have been possible from fin clippings.

The relative contribution of stocked fish to the creel in and below Massie Creek can be noted by comparing returns of stocked and native fish tagged in 1953 (Table 9). An expected greater vulnerability of the native fish to angling the first year, associated with larger size, was probably offset to some extent by an extended tagging period from April through August; whereas the hatchery fish were in the creek from early March. By midsummer of 1954, the stocked fish of age-group II should have averaged approximately 8 inches long, yet only 1.5 percent compared to 8.0 percent of the native fish were reported by anglers. Although the generally younger hatchery fish would have been expected to contribute to the fishery over a longer period, a return of only 0.2 percent was reported in 1955 and 1956 compared to a return of 2.7

TABLE 9.—*Comparison of the reported returns of hatchery-reared and native smallmouth bass released in Massie Creek during 1953 and recaptured in succeeding years by anglers*

[Percentages of the totals of tagged fish released are in parentheses]

Kind of fish	Number tagged	Length range (inches)[1]	Miles traveled	Number of tagged fish reported by anglers				
				1953	1954	1955	1956	All years
Hatchery	599	3.7–9.4	0–10	38(6.3)	2(0.3)	–	–	40 (6.7)
			10–70	8(1.3)	7(1.2)	1(0.2)	–	16 (2.7)
			Total	47(7.8)[2]	9(1.5)	1(0.2)	–	57 (9.5)
Native	112	4.5–14	0–10	8(7.1)	9(8.0)	2(1.8)	1(0.9)	20(17.8)

[1] Average lengths of hatchery and native fish were 5.1 and 8.4 inches, respectively.
[2] Includes one fish of unknown travel distance.

percent for the native fish. The downstream dispersal of a substantial number of the hatchery fish may have resulted in a reporting bias, inasmuch as anglers far downstream were less likely to report a tagged fish than were anglers familiar with project activities upstream. It can also be conjectured that the dispersing fish experienced greater natural mortality than did the native fish which were adapted to local areas.

A similar decline in returns of smallmouth bass stocked in the area upstream from Cedarville in 1955 was not necessarily caused entirely by submarginal habitat. None of those fish were recaught within less than 2 miles of release points except the single return by hoop net, and all returns by anglers except one were from points downstream from the Cedarville mill dam. The lack of returns by anglers from near stocking areas probably resulted partly from release of the fish in late October, 5 months before the start of spring fishing, and partly from limited fishing activity along the upper area. Other possible factors are as follows: (1) an average length of 7.4 inches compared to 5.1 inches for the 1953-stocked fish; (2) rearing attention such as feeding at the Newtown Hatchery in contrast to a lack of attention at the Xenia Hatchery other than removal of the fry from nests in 1952 to the larger holding ponds; and (3) the submarginal habitat which may have influenced movement and/or resulted in a high mortality rate.

The foregoing findings of this report place much uncertainty upon the stocking of yearling or late O-group smallmouth bass in streams. While not conclusive in relation to the exact value of stocking, the results emphasize the need for careful measurement of similar practices in the future. Variations between results from Massie Creek and those reported from Illinois (Larimore, 1954) indicate the complexities involved and the unsoundness of generalization or projection of results from a single stream.

ACKNOWLEDGMENTS

Appreciation is expressed to members of Project F-1-R who helped with the tagging operations, and to John Walker, Fish Management Staff Specialist of District Six, and Edward Perry, Newtown Hatchery Foreman, for making available the hatchery fish. Helpful criticisms of the manuscript were made by Clarence Clark, Supervisor of Fish Production and Investigations, Ohio Division of Wildlife; R. Weldon Larimore, Illinois Natural History Survey; and Tony Peterle, Leader of the Ohio Cooperative Wildlife Research Unit.

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Body-Scale Relationships in Landlocked Salmon, *Salmo salar*

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ABSTRACT

Scalation sequence and lengths at scale formation were determined for fry of three lake populations of salmon (*Salmo salar*). Scalation was complete for Sebago Lake salmon fry at lengths of 45 to 50 millimeters, 2 months after hatching. Average length of salmon with scales just formed was 32 millimeters. Size rather than age appears to determine time of scale formation. Linear regressions for scale length on fish length were calculated for each of four salmon populations. The body–scale relationships so calculated all differed slightly. The possibility of using a generalized correction factor in direct proportion calculations of salmon lengths at previous annuli is discussed.

INTRODUCTION

The landlocked or lake Atlantic salmon, *Salmo salar*, is one of Maine's principal cold-water game species. Found originally in only four Maine river basins (Kendall, 1935), salmon have become widely distributed since the late 19th century through efforts of fish-culturists. Early work on the landlocked salmon was confined chiefly to fish-cultural activity (Atkins, 1874), systematic studies (Kendall, 1935), and historical accounts. Considerable information was obtained about the distribution, food habits, ages, and growth of salmon during biological surveys of Maine lakes between 1939 and 1945 (Cooper, 1939a, 1939b, 1940, 1941, 1942; Cooper and Fuller, 1945; Fuller and Cooper, 1946). In 1950 inventories of salmon lakes were resumed (Everhart *et al.*, 1953), and several research projects, including growth studies, were initiated to provide technical information to improve salmon management. The purpose of the present study was to determine scalation sequence in landlocked salmon and to compare body–scale regressions in several representative salmon populations.

DESCRIPTION OF STUDY AREAS

Salmon were obtained from four widely separated oligotrophic lakes that differ considerably in size and other physical characteristics. West Grand Lake, located in Washington County, is one of a series of large lakes that drain into the St. Croix River. It has an area of 11,168 acres and a maximum depth of 128 feet. This lake is one of the original homes of the landlocked salmon (Kendall, 1935) and is one of Maine's most famous salmon waters.

Long Pond, located in Hancock County, is the largest pond in a small coastal drainage. It has an area of 897 acres and a maximum depth of 120 feet. Salmon were introduced about 1895, and the fishery is maintained largely by stocking.

Cold Stream Pond flows into the Passadumkeag River, a tributary to the Penobscot River in Penobscot County. The pond is 3,628 acres in area and has a maximum depth of 104 feet. Salmon were introduced many years ago, and the salmon fishery is maintained by natural reproduction in the outlet and by stocking.

The Fish River Lakes in Aroostook County are a group of large, interconnected lakes in the Fish River drainage, a tributary to the St. John River system. Salmon studied from this area were mostly residents of Long Lake, the headwater lake of the eastern part of the Fish River drainage (Warner, 1959). Some of the salmon, however, were residents of Cross and Square Lakes further west. Long Lake has an area of 6,000 acres and a maximum depth of 163 feet. Salmon were introduced into the Fish River Lakes in 1894 (Anonymous, 1894). An excellent salmon fishery, maintained largely by natural reproduction, has continued through the years.

Sebago Lake is also an original home of landlocked salmon. This lake, located in Cumberland County, has an area of 28,771 acres and a maximum recorded depth of 316 feet and flows into the Presumpscot River. Salmon from this lake were used only in studying scalation.

SCALATION OF SALMON

Studies of salmonids and other fishes show that scales do not arise at the same time over the body, and the sequence of scalation varies for each species (Elson, 1939; Everhart, 1949; Ward and Leonard, 1952; Pycha and

Smith, 1955). There is often a considerable variation in length at first scale formation (Everhart, 1949).

Parrot (1932) found that the average standard length of brown trout (*Salmo trutta*) at first scale formation was 35 millimeters. The scales were first observed along the lateral line slightly posterior to the dorsal fin. Scales formed anteriorly, posteriorly, dorsally, and ventrally from the point of origin. The observations of Paget (1920) and Setna (1934) were similar to those of Parrot. Elson (1939) determined that the brook trout (*Salvelinus fontinalis*) forms scale papillae at a standard length of 25 to 30 millimeters about 4 months after hatching. Robertson (1947) reported that scales first appeared on the cutthroat trout (*Salmo clarkii lewisi*) at an average total length of 46 millimeters.

In the present study scalation was observed on fry of three lake populations of salmon. Eggs were taken from adult salmon on spawning runs at West Grand Lake, Sebago Lake, and the Fish River Lakes and then hatched in three state hatcheries (Table 1). Weekly samples of 10 salmon fry from each population were preserved in a 5-percent formalin solution. Salmon fry were stained whole with alizerin red in 0.02 normal KOH (Ward and Leonard, 1952). Total length measurements were made to the nearest millimeter. Patterns of scale formation were studied with aid of a binocular microscope using 9× magnification.

Landlocked salmon scales first appear along the lateral line immediately posterior to the dorsal fin (Figure 1). The smallest salmon observed to have formed scales was 30 millimeters in total length (Table 2). The average length of 15 salmon with scales just formed was 32 millimeters. Scalation proceeds along the lateral line in both anterior and posterior directions, and, at the same time, scales form dorsad and ventrad from the lateral line. For Sebago Lake fish, scalation was complete, except for the nape and the area posterior to the pectoral fin, 2 months after hatching at a total length of 45 to 50 millimeters.

Size rather than age appears to determine time of scale formation. Nearly all the faster growing Sebago Lake fry had formed scales 7 weeks after hatching, but the slower growing West Grand Lake fry had not all formed scales until 11 weeks after hatching.

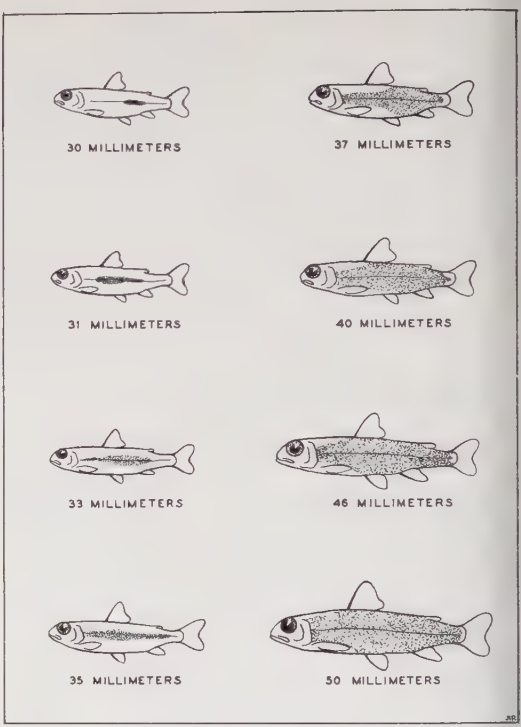

FIGURE 1.—Pattern of scalation of landlocked salmon fry.

BODY–SCALE RELATIONSHIPS

All adult salmon sampled from the Fish River Lakes and from West Grand Lake were captured during the spawning season. Most adult salmon from Long Pond and Cold Stream Pond were sampled in fishermen's creels. Salmon total lengths were measured and recorded to the nearest one-tenth inch. Van Oosten and Eschmeyer (1956) have demonstrated that total lengths are appropriate for computing growth histories from scales. Scale samples were taken from the left side of the

TABLE 1.—*Source of salmon fry used to study scalation in landlocked salmon*

Source	Hatchery	Dates (1957)		Number of collections	Range in total length (millimeters)
		Hatching	Collections		
West Grand Lake	Grand Lake Stream	April 14	May 23–June 27	6	22–39
Fish River Lakes	Enfield	April 21	June 6–June 27	3	25–32
Sebago Lake	Raymond	April 22	May 15–July 3	6	22–50

ABLE 2.—*Total length–frequency distribution at scale formation for landlocked salmon fry 25–35 millimeters in length*

Total length class in millimeters	Number examined	Number with scales	Number without scales
25	8	0	8
26	4	0	4
27	10	0	10
28	8	0	8
29	7	0	7
30	7	3	4
31	5	2	3
32	5	5	0
33	6	6	0
34	5	5	0
35	4	4	0
36	3	3	0

lmon between the origin of the dorsal fin nd the lateral line.

Anterior scale radius measurements were ade in the following manner. Several good ales from each sample were moistened with ater and temporarily mounted between glass ides. These scales were projected at 45 di- neters and their sizes and shapes carefully mpared. The anterior radius of a single od scale judged to represent the subsample as then measured to the nearest one-twentieth ch.

Everhart (1950), who worked with small- outh bass, *Micropterus dolomieui*, showed that the body length–scale length relationship computed from standard scales is not significantly different from the body–scale relationship computed from key scales. In our study we assumed that the size of the single standard scale chosen for measurement from each subsample approximated the mean size of the standard scales that comprised the total sample.

Linear body–scale regressions (Table 3) were computed using total fish lengths as the independent variables and anterior scale radii (×45) as the dependent variables. Regression equations were computed by methods described by Snedecor (1956). The calculated relationships are illustrated in Figure 2.

Slopes and equation constants for selected pairs of regressions were compared by analysis of covariance (Snedecor, 1956). All slopes or regression coefficients (b) were significantly different from one another at the 95-percent confidence level. The line elevations or equation constants (a) were significantly different for all populations except those of Long Pond and Cold Stream Pond. Thus, except for a 1-in-20 chance, the body–scale relationships for the four populations are slightly different in some respect.

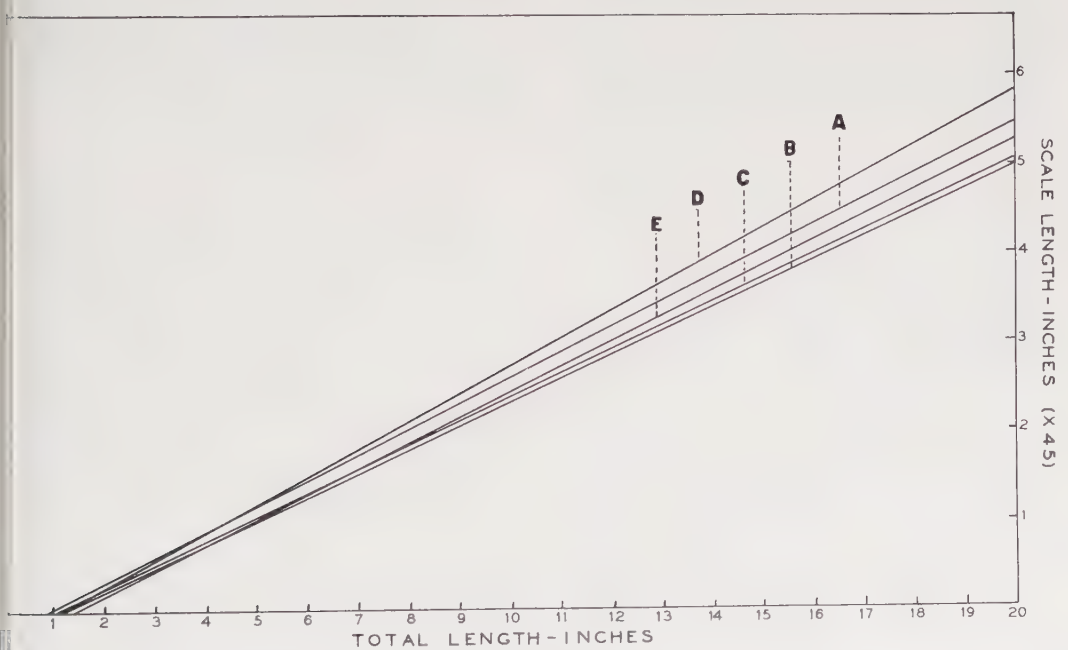

FIGURE 2.—Linear regressions of scale length on total length for landlocked salmon from four lakes and for all the lakes combined. A, Fish River Lakes; B, Long Pond; C, Cold Stream Pond; D, West Grand Lake; and E, all waters combined.

TABLE 3.—*Linear regression statistics*[1] *for body-scale relationships in four groups of landlocked salmon and for all the groups combined*

Lake	n	r	b	sb	$s_{y,x}$	Equation of regression
Cold Stream Pond	161	0.749	0.26117	0.0053	1.1937	$Y = -0.27428 + 0.26117X$
Fish River Lakes	500	0.975	0.28179	0.0028	0.4615	$Y = -0.26566 + 0.28179X$
Long Pond	211	0.928	0.26499	0.0071	0.5079	$Y = -0.27469 + 0.26499X$
West Grand Lake	240	0.969	0.30922	0.0016	0.4939	$Y = -0.35071 + 0.30922X$
Combined lakes	1,112	0.962	0.28635	0.0024	0.5289	$Y = -0.35051 + 0.28635X$

[1] n = number of fish; r = correlation coefficient; b = regression coefficient; sb = standard deviation of regression coefficient; $s_{y,x}$ = sample standard deviation from regression.

DISCUSSION

Whitney and Carlander (1956) point out that differences in body–scale relationships may be expected for the same species in different waters, and even for different year classes in the same waters. Our study material was mixed in two different ways. Several year classes were involved in the sample from each lake and none of the populations were of pure origin. Long Pond and Cold Stream Pond have been stocked with fish from both West Grand Lake and Fish River Lakes. The purest population is probably that of West Grand Lake which is an original home of the landlocked salmon and which has seldom been stocked with salmon from any other source.

While we have demonstrated a statistical difference between the body–scale relationships of salmon in these four waters, the differences, except for West Grand Lake, are small. Possibly the differences would have been more pronounced had we been able to test populations of pure origins. The equation for West Grand Lake salmon, a relatively unmixed population, is quite different from those of the other three lakes.

When body–scale growth is linear, one method of calculating lengths of fish at previous ages requires derivation of a correction factor from the body length–scale length data. The correction factor is used in the direct proportion formula, $L' = \frac{S'}{S} L$, as an adjustment for deviation of the body–scale data at hand from a 0–0 origin (Rounsefell and Everhart, 1953). Correction factors for salmon derived from our data were 1.1, 0.9, 1.0, 1.1, and 1.2 inches, respectively, for Cold Stream Pond, Fish River Lakes, Long Pond, West Grand Lake, and all the lakes combined. The correction factor for combined lakes happens to be greater than that for any of the individual lakes because these values are single-point values on the body–scale regression line (X at $Y = 0$). The regression equation is intermediate.

We used each of the individual correction factors and the correction factor from the data for combined lakes to calculate lengths at previous ages for a 12.0-inch and a 24.0-inch salmon. The calculated lengths differed only negligibly. For most routine growth work with Maine salmon populations, we believe that a generalized correction factor of 1.0 inch can be used with confidence.

Our data covered a wide range of salmon lengths. It is interesting that with our extensive sample, the X-axis intercept of the linear regression line for combined lakes (1.2 inches) closely approximated the observed length at scale formation (1.3 inches). Scale and body in landlocked salmon must grow linearly soon after scales are formed.

ACKNOWLEDGMENTS

The authors are indebted to Gerry Wade, former Superintendent of Hatcheries, and other members of the Hatchery Division of the Maine Department of Inland Fisheries and Game for their cooperation and for collection of the salmon fry. Harold E. Young deserves thanks for valuable advice and assistance on statistical procedures. Owen C. Fenderson, James S. Fletcher, and Robert M. Davis assisted with the field work and data tabulation. The Cold Stream Pond data were made available by Lyndon H. Bond and Stuart E. DeRoche. W. Harry Everhart and Robert S. Rupp reviewed the manuscript and offered constructive criticisms. The present study was partly financed through Federal Aid, Dingell-Johnson Projects, F-2-R, F-5-R, and F-11-R, Maine.

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Maturation and Spawning of the Pink Shrimp, *Penaeus duorarum* Burkenroad[1,2]

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ABSTRACT

A description is given of the anatomy of the reproductive system of male and female pink shrimp, *Penaeus duorarum*. Four stages of female maturation (undeveloped, developing, nearly ripe, and ripe) were observed using ovum size frequency, gross observation, and ratio of gonad weight to tail weight. Size of female at first sexual maturity is estimated to be about 22 millimeters (carapace length). Months of higher spawning activity are April through July. Throughout the study five ripe females were observed; four of these were found during the months of highest spawning activity. It is probable that the female pink shrimp spawns more than once during a lifetime. There is positive correlation between size of shrimp and number of ova spawned. Although temperature is the only environmental factor measured, there is reason to believe that spawning is closely associated with the annual rise and fall of bottom temperatures.

INTRODUCTION

Shrimp has become the most valuable fishery product in the United States. During 1959 shrimp landed in Florida were valued at $11.1 million. Of this yield, $3.8 million worth of pink shrimp (*Penaeus duorarum*) were taken from the Tortugas grounds (Rosen, 1960). To provide information concerning reproduction of pink shrimp, the geographic position of the main group of spawning shrimp, the size at first sexual maturity, and the number of times each shrimp spawns should be determined. Other factors involve the season of spawning and observations on the environmental factors associated with spawning. Before these parameters can be fully understood, reproductive anatomy, development of gametes, and maturation stages should be described.

MATERIALS AND METHODS

Over 5,000 pink shrimp were observed in the present study. Beginning with December 1956, 12 monthly random samples, each consisting of 200 shrimp, were collected immediately after the catch was removed from the trawl. These shrimp were preserved in 12-percent commercial formalin and borax in sea water. In this preservative tissue within the cephalothorax was often poorly preserved, although the abdomen was well preserved. The use of stronger formalin solutions was not feasible because they shrank the ova. Specimens for detailed study were preserved at sea by incising the carapace and immersing in warm Bouin's picro-formol. Material was stained in Delafield's hematoxylin and eosin, dehydrated with alcohol, and sectioned at 8–10 micra.

Frequent cruises were made aboard commercial vessels to obtain information from fresh specimens. Beginning with June 1957 an average of 195 fresh shrimp per month were examined at sea for a period of 1 year to determine the spawning season from gross observation. Three methods were used to describe the sexual development of female pink shrimp. They were gross observation of the ovaries, size-frequency distribution of eggs, and a weight–ratio method. The first method was based on changes in color, relative size, texture, and turgidity of the ovaries. Color names are based on the standard reference by Ridgway (1912). The third method was based on the fact that as a female pink shrimp became more mature, its gonads became heavier in relation to the rest of the body. Because there were difficulties in preservation, only the abdomen of the female was used. The abdominal portion of the ovaries averaged 42 percent of the weight of the whole ovary, and the abdomen 58 percent of the entire body weight. Since the rostrum of trawl-caught specimens was often damaged or was entirely missing, lengths are reported as carapace length, or the distance from the orbital depression of the carapace to the most

[1] From a M.S. thesis at The Marine Laboratory, University of Miami, Florida. Financial assistance was received from the Shrimp Association of the Americas and the Florida State Board of Conservation.

[2] Contribution No. 328 from The Marine Laboratory, University of Miami.

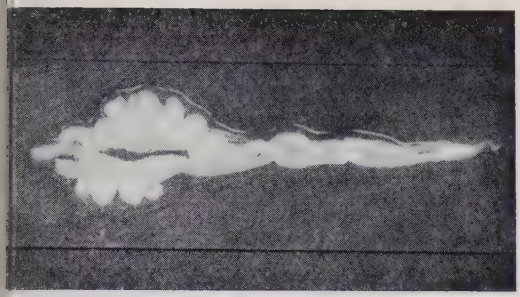

FIGURE 1.—Early developing ovaries from a fresh female with six right and seven left lateral lobes—12×.

dorsoposterior end of the carapace.

Male shrimp were not used to indicate spawning activity because a satisfactory method for determining the stage of maturity of the male has not yet been devised, and because the testes are entirely within the cephalothorax, which is difficult to preserve.

ANATOMY OF THE REPRODUCTIVE SYSTEM

The reproductive system of the female pink shrimp consists of paired ovaries, oviducts, external genital apertures, and a thelycum. In one case a 29-millimeter female completely lacked ovaries and oviducts but exhibited normal external sexual characteristics. Ovaries extend from the anterior wall of the cephalothorax to the telson. The relative size, color, and texture of ovarian tissue is dependent upon the degree of maturity. Each ovary has one anterior lobe and from six to eight lateral lobes in the cephalothorax and one large lobe in the abdomen (Figure 1). Abdominal lobes are contiguous with the gut, which is situated between and below them (Figure 2). The oviducts originate at the tips of the sixth or seventh lateral lobes and descend to the external genital apertures hidden in the ear-like lobes at the coxae of the third pair of pereiopods (Figure 3).

The thelycum is situated between the bases of the fifth pair of pereiopods. Impregnation of soft, newly moulted females can usually be detected by gross inspection. The thelycum of such a specimen is dark orange and swollen, and often the edge of the spermatophore mass protrudes between the two halves of the thelycum. In any case, examination of a smear from the contents of the thelycum will verify the presence of sperm.

The paired testes of male pink shrimp lie in the cephalothorax and have lateral lobes which descend over the hepatopancreas. The

FIGURE 2.—Cross section through a developing female showing ventral part of left ovary with developing ova in proximity to the gut (lower right)—62×.

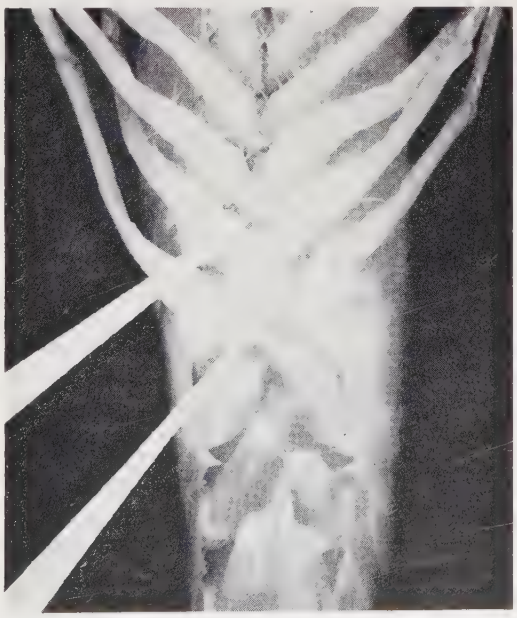

FIGURE 3.—Ventral view of female with top pointer on the external genital apertures, bottom pointer on left half of thelycum. Pleopods are excised for clearer view—1.5×.

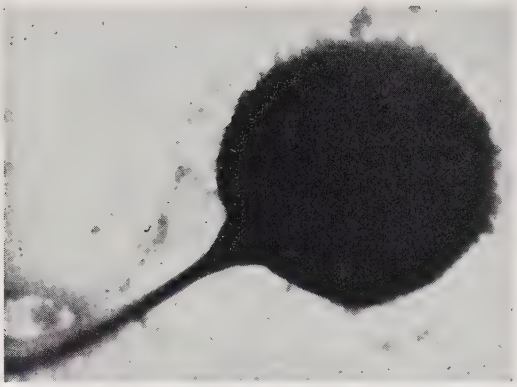

FIGURE 4. — Spermatozoan from a 32-millimeter male photographed with the electron microscope. Fuzzy outline is an artifact caused by electron bombardment—8,150×.

last lateral lobe leads to the vas deferens, which carries spermatozoa to the terminal ampoule, located at the posterior base of the last pereiopod. The vas deferens has three distinct areas (proximal, medial, and distal), and in mature specimens it is about 0.5 millimeter in diameter. The spermatozoan has a head that is nearly spherical, a small midpiece, and a flagellum that is about as long as the head is wide (Figure 4).

Only rarely were male shrimp seen with the spermatophore mass entangled in the petasma and protruding from the terminal ampoule (Figure 5). It is believed that sperm transfer takes place between a hard male and a soft female because only hard males were seen with extruding spermatophores; only soft females exhibited an appearance of being recently impregnated; parts of the spermatophore were seen in cast-off shells from females; even with a fresh specimen, it is difficult to open the thelycum of hard females; and the literature on other penaeid shrimps (Hudinaga, 1942) indicates that impregnation occurs between hard males and soft females.

MATURATION OF THE FEMALE

Size of ova is not significantly different in the anterior, middle, and posterior areas of the ovary. Although an analysis of variance revealed no significant difference in means among the three subclasses at the 1-percent level of significance, with N being 126, 128, and 100, respectively, ova were always removed from the anterior region of the abdominal lobes. Preserved ova are polymorphic and a method of random measurement was

FIGURE 5.—(A) Pointer directed to spermatophore mass entangled in the copulatory organ of a male. (B) Male with no extruding spermatophore, needle under copulatory organ. Pleopods excised for clearer view—0.62×.

adapted from Clark (1934). More information on the developing group(s) of ova was obtained by measuring only those as large as six units of ocular micrometer (1 unit = 0.0137 millimeters).

"Weight ratio" is the percentage of total abdominal weight represented by the weight of the abdominal lobes of the ovary. A test for independence was made of the data from 85 female shrimp of random size in order to compare ovum-size frequency and weight ratio. The null hypothesis that the two variables are independent was tested and rejected at the 0.1-percent level, with $r = 0.655$. Where $X =$ modal value of egg diameters and $Y =$ weight ratio, the line of best fit is represented by the equation

$$\text{Log}_{10} Y = 1.583 \ \log_{10} X + 0.149 .$$

The maturation process has been arbitrarily categorized into four successive stages of development for the purpose of describing the degree of sexual maturity.

Undeveloped stage

Ovaries in this stage (Figure 6A) are very small in relation to other organs. They are translucent, very flaccid, difficult to remove, and invisible through the exoskeleton. Ova from undeveloped females are relatively small and translucent, and only the largest eggs reveal a nucleus and yolk granules (Figure 7A). Figures 8A and 8B represent pooled size frequencies of ova of undeveloped shrimp. The modal value is less than 10 units, and there is no separate group of developing ova. The weight ratio of undeveloped shrimp varied from 0.15 to 1.2 within the size range usually

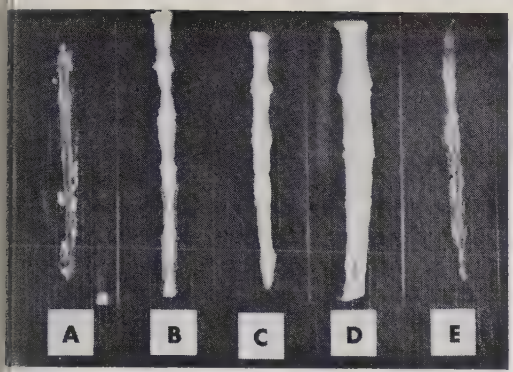

FIGURE 6.—The same section from abdominal lobes preserved female pink shrimp. (A) undeveloped, (B) developing, (C) nearly ripe, (D) ripe, and (E) believed to be spent.—0.50×.

aught by commercial vessels (greater than millimeters).

Developing stage

Developing ovaries can easily be differentiated from other tissue. They are flaccid and relatively larger than undeveloped ovaries (Figure 6B). Fresh ovaries are white to pale olive buff, while preserved tissue, in order of maturation, varies from white to baryta yellow. As the ovum develops more protein accumulates, the tissue becomes opaque, and in whole ova the nucleus disappears from view (Figure 7A). Developing ova have yolk granules and cells believed to be nutritive bodies (Figure 7B) and have a range of modal sizes from 10 to 20 micrometer units. By definition, the developing stage begins when a separate group of developing eggs separates from the stock of small eggs (Figures 7C, 8D, 8E). The weight ratio of developing shrimp had a range from 1 to 3 percent, with much overlap into the next stage.

Nearly ripe stage

This stage may be accurately determined in the field because fresh ovaries are a glaucous color, which is darker in more mature ovaries. Preserved ovaries are dark buff. Nearly ripe ovaries of fresh shrimp are visible through the exoskeleton and are large (Figure 6C) and slightly turgid. Preserved ovarian tissue is very turgid. Nearly ripe ova from unsectioned material are opaque (Figure 7C), and the modes of size-frequency distributions generally fall between 20 and 25 units (Figures 8F, 8G).

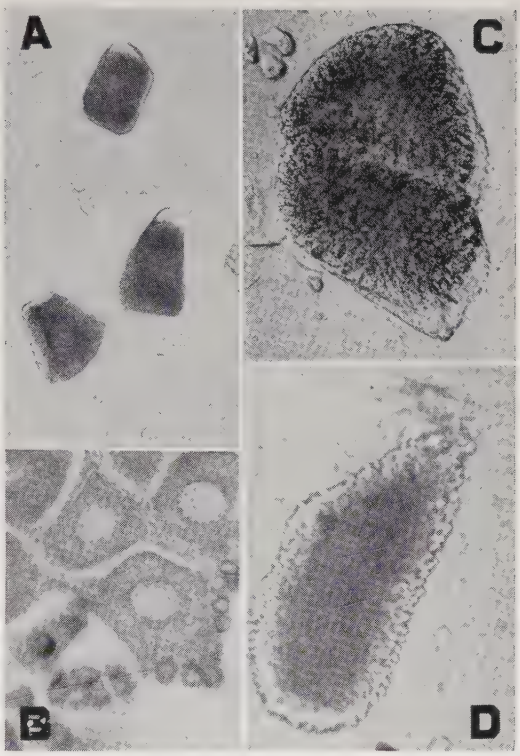

FIGURE 7.—(A) Three preserved, late developing ova with numerous undeveloped ova—131×. (B) Cross section of developing ova with yolk granules around the nuclei. Small cells are believed to be nutritive in function—186×. (C) Two preserved, nearly ripe ova. In the whole ovum of this stage the nucleus eventually disappears from view—171×. (D) A preserved, ripe ovum with peripheral rod-like bodies which are believed (Hudinaga, 1942) to contain the jelly-like material used as a covering for the ovum at the time of extrusion—90×.

Ripe stage

The ripe stage can be distinguished from the nearly ripe stage only by the presence of a characteristic margin of peripheral rod-like bodies, the apexes of which appear to radiate from the center of the egg (Figure 7D). It is believed that this is the final stage before the actual spawning of pink shrimp because: (1) of 300 specimens examined during a 12-month period, four of the five females in the ripe stage were caught during the months believed from other evidence to be the major spawning period; (2) shrimp of this stage contained the largest ova encountered (the mean modal size of the developing group of ova was 27 units (Figure 8H), or 4.37 millimeters, and the weight ratio averaged 3.5 percent); and (3) the literature on

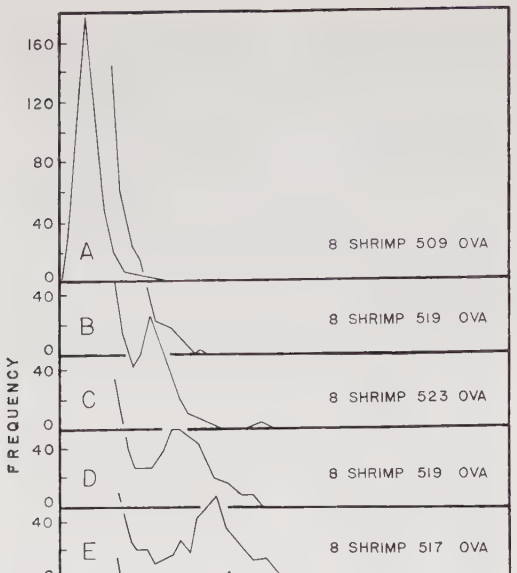

FIGURE 8.—Graph showing pooled average size–frequency distributions of ova of preserved female pink shrimp in order of the maturation process. Data are purposefully taken from specimens throughout the 12-month period of observation.

other penaeid shrimp reports the presence of peripheral bodies as indicative of the ripe stage (Hudinaga, 1942; King, 1948).

With the exception of an occasional specimen with some large ova undergoing resorption, no satisfactory method was found to identify spent females. J. E. King, in personal communication, stated that in white shrimp this characteristic was the most useful indication of spent individuals, and that a recovery stage occurred during which it was not possible to recognize shrimp which had already spawned.

SIZE AT FIRST SEXUAL MATURITY

To estimate the size at first sexual maturity the size of all female shrimp with modal values of the developing ova greater than 20 units, or 0.27 millimeters, was recorded from the 12 consecutive monthly samples. All of these specimens were in the early ripe or ripe stage. Although shrimp as small as 18 millimeters were sampled, the smallest early ripe or ripe shrimp was 24 millimeters. By plotting the size of shrimp in 1-millimeter groupings (X) against the percentage of the total number of shrimp in each group (Y), a regression was made of data from shrimp up to 33 millimeters in length. By extrapolation the X intercept was 22 millimeters, and this is the estimated size at first sexual maturity.

Information from Durbin Tabb of the University of Miami indicates that 22 millimeters is slightly greater than the size at which most juveniles leave the nursery grounds in Everglades National Park, presumably headed for deeper offshore waters. This estimate of the size at first maturity is a little larger than the figure of 18.6 millimeters given by Eldred (1958) as the size at which pink shrimp are capable of being impregnated.

SPAWNING SEASON

Two methods were used to estimate the season of spawning—a regression analysis involving gonad weight and tail weight, and the gross observation of fresh specimens. Of the two methods, the latter appears to give the best estimates. Although sampling began in January 1957, it was not until June of that year that confidence could be placed in the gross observation of fresh material to describe sexual maturity. In the interim, descriptions of fresh specimens were made at sea. Specimens were then labeled, preserved, and brought to the laboratory to relate stage of maturity with the appearance of fresh material.

Beginning with June 1957, gross observations of fresh shrimp were begun throughout the Tortugas area. Sampling continued for 12 successive months except September and October 1957, when no observations of fresh specimens were made. The resulting data indicate that the months of highest spawning activity are April through July (Figure 9). Working in a restricted area of Tortugas, Ingle *et al.* (1959) give a similar estimate for 1958.

Gross observation of fresh material does not allow the separation of ripe from early ripe shrimp; "greenness" of the ovaries, however, does indicate that a female has at least attained the early ripe stage. Consequently, it is assumed that the season of the year when the highest frequency of glaucous-colored

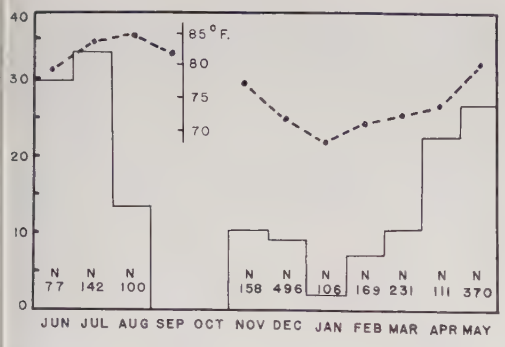

FIGURE 9.—Graph of the spawning season as revealed by the percentage of nearly ripe and ripe males in the samples from the Tortugas grounds during the year 1957–58. Superposed temperature data reveal a correlation between temperature and spawning.

varies occurs closely approximates the season of highest spawning activity. Four of the five ripe females occurred at this time, and the fifth occurred during September, for which no data from fresh shrimp are available. Furthermore, 2 years following the completion of the present work, unpublished data on the appearance of pink shrimp larvae on the Tortugas grounds support the present estimate of the season of highest spawning activity (personal communication with Sheldon Dobkin of The Marine Laboratory).

Two implications arise from the fact that some early ripe shrimp were found throughout the year. Either there is some spawning throughout the year, or some females can remain in the early ripe condition for a long time preceding actual spawning. A more accurate determination of the spawning season will result from present studies being conducted at The Marine Laboratory on the numbers of ova and larvae.

Many authors, for example Marr (1955), advocate the use of a regression technique for studying the relative growth of body parts instead of averages of ratios which may lead to "erroneous interpretation." Although such a regression (gonad weight (X) on tail weight (Y)) was made for each one of 12 monthly samples (January–December 1957), the results are not clear. Apparently these data do not yield readily to a regression analysis even though individual weight ratio is significantly correlated with the stage of maturity as shown by size frequency of ova. One reason may be relatively low r values; another the small range in shrimp size for any one month. Insignificant and negative r values, however, were recorded during the spawning season (Figure 9). The greatest range in Y values would be expected during this period for any given value of X, since ripe and spent females are on the grounds at the same time. Conversely, a higher value of r occurs during the winter months, when the weight of the gonads is not relatively high in some shrimp and low in others. November, December, January, and February are not associated with a high frequency of early ripe shrimp nor is a large number of spent females to be expected at this time. The combination of these two factors would tend to reduce r. The data for maturity stages are inadequate for a comparison of geographic area and spawning activity.

TABLE 1.—*Mean bottom water temperatures for the Tortugas grounds*[1]

Date	Number of observations	Temperature (° F.)	Mean depth (feet)
January 1957	8	79.9	100.9
July 1956	6	84.0	74.0
August 1956	7	85.3	87.4
September 1956	7	82.3	78.6
October	–	–	–
November 1955	4	77.5	80.0
December 1955	6	72.1	81.3
January 1957	5	68.5	77.0
February 1956	6	71.1	81.7
March 1956	6	72.4	82.5
April 1956	5	73.8	80.0
May 1957	2	79.8	95.0

[1] These data were read from bathythermograph slides collected by James Regan and James Alexander of The Marine Laboratory, University of Miami.

SPAWNING AND TEMPERATURE

The occurrence of early ripe and ripe pink shrimp and the temperatures of bottom waters on the Tortugas grounds are highly correlated (Figure 9). In the case of white shrimp, *Penaeus setiferus*, Lindner and Anderson (1956) report a similar correlation between water temperature and spawning. Temperatures reported here are for the same months as the maturity data, but most refer to the previous year (Table 1). Temperature records were unavailable for the entire year June 1957–May 1958; however, there is little reason to believe that the annual cycle of temperature would change appreciably. It is widely known that temperature is a triggering mechanism for the spawning of many invertebrates. Temperature is the only environmental factor considered during the study, and it is not implied that the correlation is one of cause and effect.

MULTIPLE SPAWNING

Multiple spawning is not uncommon among penaeid shrimp. It is believed that both *Pe-*

TABLE 2.—*Date, location, and size of ripe pink shrimp females collected*

Size (millimeters)	Date (1957)	Position
32.7	April 13	180 feet depth, south of Loggerhead Light
26.7	June 11	Tortugas
30.0	July 16	68 feet depth, 280° Key West
28.9	July 16	68 feet depth, 280° Key West
36.6	Sept. 18	South, southeast Rebecca, one hour

naeus japonicus and *Penaeus setiferus* spawn more than once during their life (Hudinaga, 1942; Lindner and Anderson, 1956). The only evidence for pink shrimp spawning more than once is one of the ripe females whose ovum-size frequency showed two developing groups in addition to the stock of undeveloped ova. Peripheral bodies were found only in the group with a modal value of 29 units. These ripe ova were the largest encountered during the study. Either further growth in the other ripe females examined would have produced a second group of developing ova, or having spawned before, these shrimp were producing their last group of ripe eggs. The second case seems more plausible since the specimen shown to contain two groups of developing ova was the first ripe female encountered during the spawning season (April, Table 2). Whether or not multiple spawning actually exists in the population, there are data (Figure 10) which support the conclusion that larger females produce a greater number of ova.

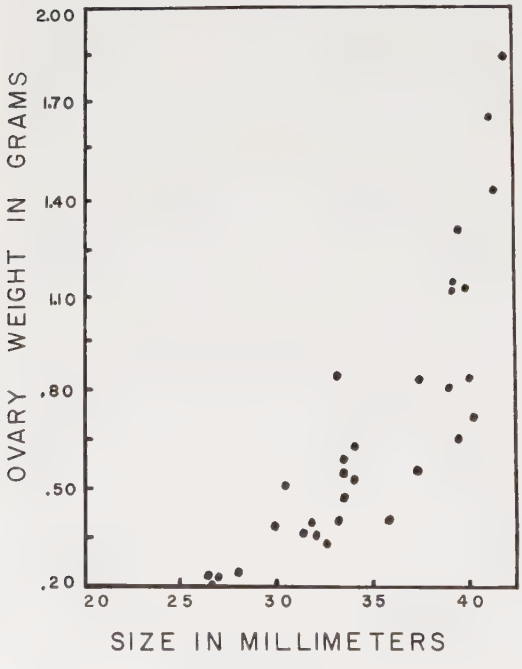

FIGURE 10.—A plot of ovary weight against shrimp size from 31 nearly ripe females sampled during the spawning season.

ACKNOWLEDGMENTS

The author is grateful to C. P. Idyll and E. S. Iversen of the Institute of Marine Science, University of Miami, for suggesting the problem and for continued guidance; to the members of the fisheries staff who assisted in obtaining samples; and to Albert C. Jones for his valuable criticism of the manuscript. Appreciation is extended to numerous members of the Key West shrimp fleet for their cooperation in obtaining samples. Many thanks also go to Claude F. Carter for suggestions with the electron microscopy, and to Saul B. Saila of the University of Rhode Island for his help with the computation.

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Influence of Water Exchange and Dissolved Oxygen in Redds on Survival of Steelhead Trout Embryos[1]

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ABSTRACT

A field study of spawning gravel conditions affecting the survival of steelhead trout (*Salmo gairdneri* Richardson) embryos was conducted in two small streams in the Alsea River Basin in Lincoln County, Oregon, from February to June 1959. Holes 10 inches deep, approximating natural redds, were dug in arbitrarily selected spawning locations. Plastic mesh sacks containing gravel and 100 fertilized trout eggs were placed in the upstream end of each hole. A standpipe was placed in the lower end of each excavation about 10 inches away from the eggs, and the hole was filled with gravel to the streambed level. Periodically, determinations were made of gravel permeability and of the apparent velocity and dissolved-oxygen content of the intragravel water. A month after calculated hatching times, the bags were removed from the streambed, and the fry contained in them were counted and preserved. The permeability of the spawning gravel fluctuated while embryos were in the gravel. During this period mean gravel permeabilities ranged from 80 to 400 meters per hour; apparent velocities from 5 to almost 110 centimeters per hour; and dissolved-oxygen concentrations from 2.6 to 9.25 milligrams per liter. Embryonic survival percentages ranged from 16 to 62. There was positive correlation between the apparent velocity of ground water and embryonic survivals, and between the dissolved-oxygen levels of the gravel water and survivals. Apparent velocities and dissolved-oxygen concentrations were closely related in the intra-gravel water, and effects of these factors could not be separated.

INTRODUCTION

In 1958 the Oregon Cooperative Wildlife Research Unit[3] and the Governor's Committee on Natural Resources[4] initiated studies on the effects of logging practices upon various watershed values in Lincoln County, Oregon. One study included several years of investigation of salmonid production in three streams of the Alsea River Basin, Needle Branch, Flynn Creek, and Deer Creek, which drain areas of uncut Douglas fir forest. The phase of the study reported here was designed to provide information on conditions in spawning gravels before the streambeds become altered as a result of logging. Most of the work was done on Needle Branch. A few experiments were conducted in Horse Creek, a small stream which drains a logged area. Gravel in the streambeds is mostly sandstone. In sections of the streams used by salmonids for spawning, there are few rocks larger than 4 inches in diameter. Redds are dug in bottoms which range from silt to particles 3 inches in diameter.

This coastal area receives an annual rainfall of about 100 inches per year, most of which falls between October and May. Water levels in the streams fluctuate greatly during this 8-month period, and considerable movement of streambed gravels occurs, especially during peak flows. Water temperature and discharge data for Needle Branch are presented in Table 1. The temperature of the water below the surface of the streambed was virtually the same as that above it.

The term "embryo" is used herein to specify all stages of development from fertilization to the time of fry emergence from the gravel. Some conditions in spawning beds that affect the fate of embryos within them are gravel permeability, a characteristic of the gravel itself, and apparent velocity and dissolved oxygen, characteristics of the water flowing through the gravel. "The *apparent velocity* sometimes called the superficial or macroscopic velocity, is the rate of seepage expressed as the volume of liquid flowing per unit time through a unit area (of solids plus voids) normal to the direction of flow. The *true*, or *pore velocity* is the actual velocity of flow through the interstitial spaces, and differs from pore to pore" (Pollard, 1955). For

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[3] Oregon State College Agricultural Research Foundation, Wildlife Management Institute, U. S. Fish and Wildlife Service, and Oregon State Game Commission cooperating.

[4] Comprised of representatives of various State agencies that are concerned with the conservation of Oregon's natural resources.

TABLE 1.—*Maximum and minimum discharges and water temperatures of Needle Branch, Lincoln County, Oregon, 1959*[1]

Month	Discharge (cubic feet per second)	Temperature (degrees Fahrenheit)
January		
Maximum	14.0	48
Minimum	1.7	41
February		
Maximum	7.8	48
Minimum	1.3	42
March		
Maximum	4.8	48
Minimum	0.7	44
April		
Maximum	3.7	51
Minimum	0.3	45
May		
Maximum	3.7	51
Minimum	0.4	46
June		
Maximum	1.0	54
Minimum	0.3	48

[1] Obtained from a stream gauge operated by the U. S. Geological Survey.

present purposes, permeability is defined as the capacity of the gravel to transmit water. Spawning gravels, depending on their nature, transmit water at various rates, and in this paper the capacity to transmit water is expressed in meters per hour.

Wickett (1954) found low dissolved-oxygen concentrations attributed to low water flow in portions of a study stream and thought they may have caused the observed high mortalities of chum salmon (*Oncorhynchus keta*) embryos. He also described a standpipe (later improved by Terhune, 1958) which was used to estimate the apparent velocity of the intra-gravel water, and which provided access to water for dissolved-oxygen determinations. Alderdice, Wickett, and Brett (1958) exposed chum salmon embryos to low dissolved-oxygen levels for 7-day periods and then held the embryos at saturation levels for the remainder of development. Various concentrations at different developmental stages resulted in delays in hatching, abnormal development, and increased mortalities. Silver[5] held steelhead trout (*Salmo gairdneri*) embryos and chinook salmon (*Oncorhynchus tshawytscha*) embryos from fertilization to hatching at various concentrations of dissolved oxygen and at known velocities of water current. Reduced levels of dissolved oxygen or velocity caused delays in hatching, and the fry produced at the low levels were smaller in length and volume at hatch than those reared at higher levels of dissolved oxygen or water velocity. Shumway[6] also found that the production of embryonic tissue was reduced with decreased levels of dissolved oxygen or water velocity.

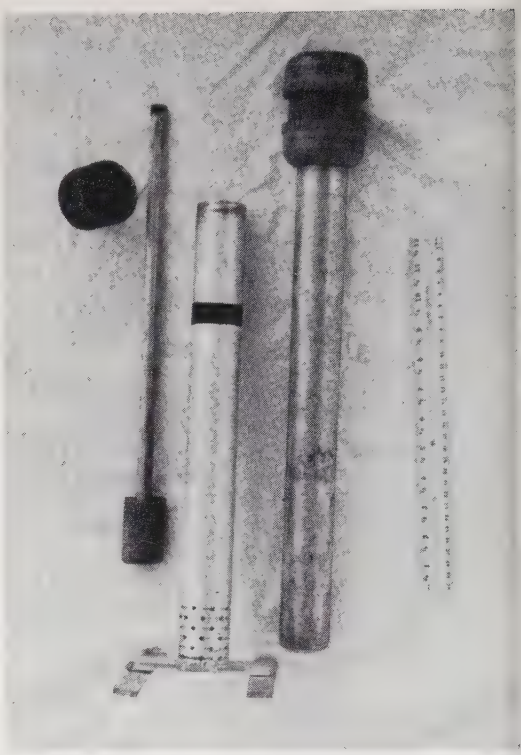

FIGURE 1.—The standpipe assembly showing extension, stopper, and cap.

MATERIALS AND METHODS

Standpipes, which have been used for studies of water flowing through gravel, are pieces of pipe perforated at one end which, when placed vertically in a streambed, permit ground water to flow through the lower end. The top of the pipe extending above the surface of the stream provides access to the intragravel water. Standpipes used in this study (Figure 1) were 15-inch lengths of 1¼-inch aluminum pipe perforated in the lower 2 inches by 48 ⅛-inch, evenly spaced holes. The

[5] Silver, S. J. (1960) The influence of water velocity and dissolved oxygen on the development of salmonid embryos. M.S. thesis, Oregon State College, Corvallis. 50 pp.

[6] Shumway, D. L. (1960) The influence of water velocity on the development of salmonid embryos at low oxygen levels. M.S. thesis, Oregon State College, Corvallis. 49 pp.

lower end was sealed by a small plate, and two flat metal bars attached here served to hold it more firmly in the gravel. Horizontal grooves one-sixteenth inch wide and one-sixteenth inch deep extended between the holes on the outer surface of the pipe and reduced the chance of pebbles blocking the openings. A piece of sponge rubber on a handle could be placed in the standpipe to prevent water from flowing through the pipe when it was not in use. When the pipe with top capped was buried 10 inches in the gravel with the stopper in place, it could be considered a part of the streambed. When measurements of intra-gravel conditions were being made, the cap and stopper were removed, and a 2-foot extension was fitted to the top of the pipe.

This standpipe incorporates some of the features of the pipe developed by Gangmark and Bakkala (1958) and the one designed by Terhune (1958). In these two papers and the paper of Pollard (1955), there are complete discussions of the theories behind and the limitations involved in the design, calibration, and use of standpipes.

Gravel permeability can be estimated through its relationship to the rate at which water can be removed from a standpipe by pumping. When water is pumped from a standpipe into a graduated cylinder and the time taken to remove it is recorded, an amount of water per unit of time is obtained, and this is a function of the permeability of the gravel surrounding the pipe. The relationship between the rate of water removal and the permeability of the gravel has been shown by Terhune (1958).

The apparent velocity of the ground-water flow can be estimated from the relationship between the rate of flow in the lower end of a standpipe and water velocity in the streambed. When a color solution is injected into a standpipe, the color of the water in the pipe becomes lighter with time as it is diluted by exchange with water from the streambed. By periodic sampling of water in the pipe, the rate of dilution may be measured. Apparent velocity of the water flowing through the streambed can then be estimated from the relationship of dilution rate to ground-water flow (Terhune, 1958).

Dissolved-oxygen determinations were made on 37-milliliter samples of water taken from the pipes (Harper, 1953).

On February 10, 1959, fertilized steelhead trout eggs were obtained from the Oregon Fish Commission hatchery on Fall Creek, a tributary of the Alsea River, and transported directly to the study area, a distance of 65 miles. Holes 10 inches deep and about 14 inches long were dug in spawning gravel at arbitrarily selected locations.[7] Gravel and water-hardened eggs (100 per sack) were placed in plastic mesh sacks having 19 meshes per inch, and the tops of the bags were secured with nylon cord. A standpipe was placed in the downstream end of each hole, and a sack of fertilized eggs and gravel was put in the upper end about 10 inches away from the pipe. The hole was then filled with gravel to the level of the streambed. Determinations of gravel permeability and of apparent velocity and dissolved-oxygen content of ground water were made at intervals throughout the incubation period. One month after calculated hatching times, the sacks and pipes were removed and fry in the sacks counted and preserved in Bouin's solution. Silt was deposited to various degrees on the mesh of many of the sacks. The effect of it on water circulation through the bags was not determined but was thought to be of little importance to the survival of the embryos.

RESULTS

The first measurements from the standpipes were taken 2 days after the study redds were prepared. A permeability measurement was made each week (except one) for the next 12 weeks, and 10 apparent velocity determinations were obtained in this period. Various numbers of dissolved-oxygen determinations were made at different stations. The permeability of the gravel surrounding the standpipes continually changed during the incubation period (Table 2). The environment of the embryos is by no means stable.

From more complete data in two study redds in Horse Creek and eight in Needle Branch (Table 3), it can be noted that conditions were quite different in the various redds. Mean permeabilities ranged from 80 to 400 meters per hour, mean apparent velocities from 5 to 108.5 centimeters per hour, and mean dissolved-oxygen concentrations from 2.6 to 9.2 milligrams per liter. Survival percentages ranged from 16 to 62. The relationships between these environmental conditions and the survival of the embryos is more clearly illustrated in Figures 2 and 3. In these figures the regression lines are drawn

[7] Subsequently wild fish dug redds in some of the chosen areas.

TABLE 2.—*Permeability measurements in meters per hour from Horse Creek and Needle Branch, 1959*

Date	Station									
	Horse Creek		Needle Branch							
	1	2	1	2	3	4	5	6	7	8
February										
12	100	350	150	60	350	200	350	350	90	350
19	100	200	200	100	500	150	450	450	100	500
26	150	150	150	60	450	200	300	450	150	300
March										
5	60	100	150	100	350	100	300	200	60	300
12	60	150	150	60	300	100	200	200	100	150
20	100	150	150	100	150	100	150	150	60	150
28	60	100	150	100	150	60	200	200	60	150
April										
2	100	150	150	60	100	90	150	100	60	150
16	60	150	150	60	200	60	500	500	100	200
23	60	150	150	100	150	60	450	500	60	200
May										
1 or 13	70	90	150	200	150	70	550	350	40	300
1 or 13	70	200	100	90	100	80	700	800	50	350

between the means of the five highest and the five lowest observations. In Figure 2 percentages of survival are plotted against the mean apparent velocities. In general low embryonic survivals are associated with low mean velocities, and higher survivals with higher velocities. In Figure 3 the percentages of survival are plotted against the mean dissolved-oxygen concentrations. Here, low survivals are shown to be associated with low mean dissolved-oxygen levels, and higher survivals with higher oxygen concentrations. No relationship between permeability and survival was found.

DISCUSSION

In this study the determinations of apparent velocity and of dissolved oxygen were of similar value for appraising the environment of the embryos. In Figure 4 the relationship between the apparent velocity of ground water and embryonic survival has been removed by adjusting the percentages of survival to what they might have been at 31 centimeters per hour, the mean value of all apparent velocity determinations. This is essentially a graphic method of multiple regression analysis. The adjusted percentages of survival are plotted against the 10 mean dissolved-oxygen values, and no definite relationship is apparent. If a positive correlation were shown here, the dissolved-oxygen data would be accounting for more effects of the environment on the embryos than were the velocity measurements. In Figure 5 the relationship between dissolved oxygen and survival has been removed by adjusting the percentages of survival to what they might have been at 6 milligrams per liter of oxygen, the mean value of all dissolved-oxygen measurements. These adjusted percentages of survival are plotted against the 10 mean apparent velocity figures. Since a positive correlation is not obvious here, the velocity determinations account for no environmental effects not already accounted for by the measurements of dissolved oxygen.

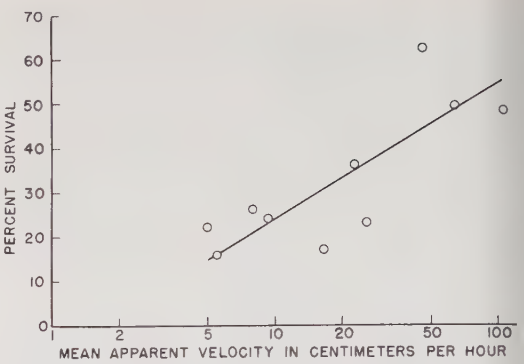

FIGURE 2.—The relationship between apparent velocity and embryonic survival.

The relationship between dissolved-oxygen concentration and apparent velocity in the

TABLE 3.—*Permeabilities, apparent velocities and oxygen concentrations of water, and percentages of survival of steelhead trout embryos in 10 study redds in Horse Creek and Needle Branch*

Station[1]	Permeability (meters per hour)		Apparent velocity (centimeters per hour)			Oxygen (milligrams per liter)			Percentage survival
	Mean	Range	Mean	Minimum	S.D.	Mean	Minimum	S.D.	
H.C. 1	82.5	60–150	26.0	12.5	10.3	5.7	3.9	1.9	23
H.C. 2	160	90–350	9.5	2.5	6.1	6.5	4.1	2.1	24
N.B. 1	150	100–200	8.0	5.0	2.9	5.2	4.1	1.2	26
N.B. 2	90	60–200	16.8	10.0	4.4	6.4	4.0	1.7	17
N.B. 3	245	100–500	65.0	30.0	32.2	6.4	3.8	2.0	49
N.B. 4	105	60–200	5.5	2.5	1.9	2.6	1.0	1.9	16
N.B. 5	400	150–700	23.0	17.5	12.8	8.3	3.6	2.6	36
N.B. 6	355	150–800	5.0	2.5	2.7	2.7	0.8	1.8	22
N.B. 7	80	40–150	46.5	15.0	17.8	9.2	7.4	1.9	62
N.B. 8	300	150–500	108.5	85.0	21.1	6.6	4.1	3.4	48

[1] H.C. = Horse Creek; N.B. = Needle Branch.

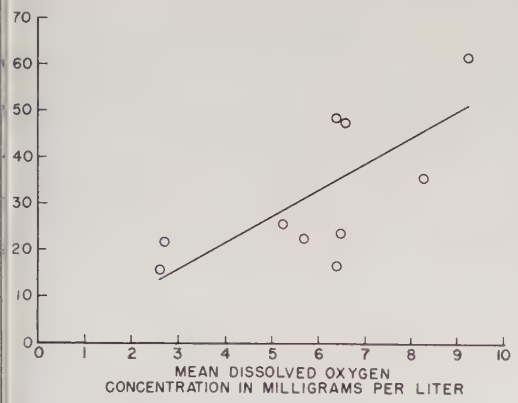

FIGURE 3.—The relationship between dissolved-oxygen concentration and embryonic survival.

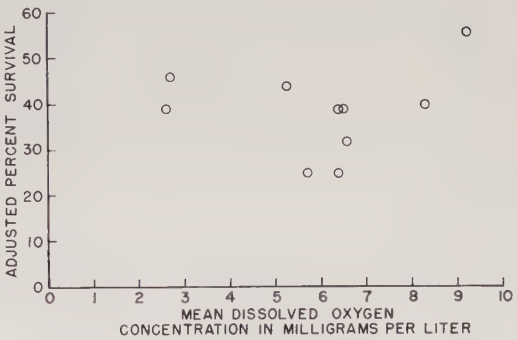

FIGURE 4.—The relationship between dissolved-oxygen concentration and the percentage of survival adjusted to 31 centimeters per hour apparent velocity to remove velocity relationship.

reambed is indicated in Figure 6, in which ie regression line is drawn by eye. It is apparent that when velocities are low, oxygen oncentrations may be expected to be low; id when they are higher, oxygen levels may e expected to be higher.

The apparent similarity in the value of oxyn concentration and apparent velocity for dicating the suitability of the embryonic enronment can be misleading. It is oxygen at is essential to the embryo, and the funcon of water movement is mainly to deliver xygen to the embryo and to carry away etabolic waste products. Shumway[8] found at the embryo's oxygen requirements can be et by very low water velocities when oxygen oncentrations are adequate and that the inuence of different velocities ranging from 3 750 centimeters per hour on embryonic rowth is slight compared to the influence of xygen levels ranging from 2.5 to 10.3 milirams per liter.

In the streams studied, determinations of e oxygen content of water flowing through e redd apparently provide the information ecessary for a satisfactory evaluation of the nvironment of the embryos. Situations may ccur where oxygen levels are low while vecities are high because of the flow pattern the gravel or because there are large mounts of organic matter or large numbers f embryos in the gravel. In these instances xygen determinations would be the only satfactory means of evaluating the environent. In two redds receiving waters flowing t different velocities but having the same oncentration of dissolved oxygen, conditions for embryonic development may be better in the area with the higher exchange rate of water.

It was found during the study that gravel 6 inches away from a standpipe had little effect on the permeability measurement obtained at the pipe, and that gravel permeability varied greatly from point to point. Sometimes standpipes half a foot apart yielded different readings, even though measurements taken one after another at either pipe were the same. The velocity of subsurface flow is mostly a function of the hydraulic head and the permeability of the gravel. Therefore, a closer relationship between velocity and survival than between permeability and survival and the observed lack of apparent relationship between gravel permeability and survival would be expected. Over a relatively large area, however, a positive correlation between permeability and survival may generally be ex-

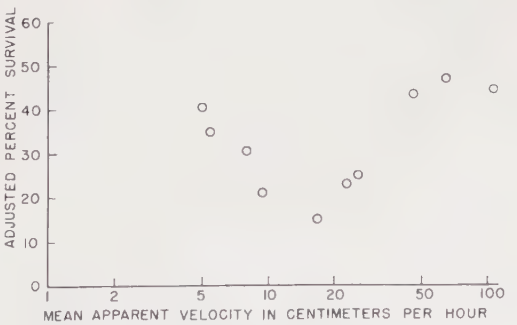

FIGURE 5.—The relationship between apparent velocity and percentage of survival adjusted to 6 milligrams per liter of dissolved oxygen to remove oxygen relationship.

[8] See footnote 6.

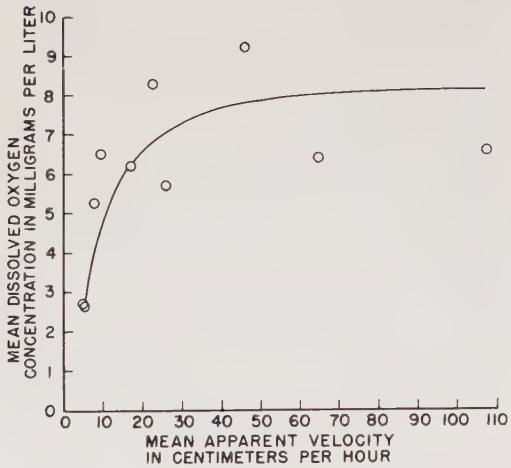

FIGURE 6.—The relationship between apparent velocity and dissolved-oxygen concentration.

pected. Wickett (1958) states that "the density of spawners that produces the greatest numbers of fry is related to the average permeability of the stream bottom."

Indications were found that considerable gravel movement occurs at least 10 inches below the streambed during the period that salmonid eggs are in the gravel. This shifting gravel as well as insufficient oxygen may be a cause of egg losses. Gangmark and Broad (1956) found early mortalities corresponding with freshets. No information pertaining to this question was acquired in this study.

ACKNOWLEDGMENTS

I wish to thank Arthur S. Einarsen, leader of the Oregon Cooperative Wildlife Research Unit and Homer Campbell of the Oregon State Game Commission for assistance throughout the study; Donald Chapman for invaluable advice in planning the experiment and for assistance with the field work; Charles E. Warren for assistance in the evaluation of the data and for criticism of the manuscript; Lyle Calvin for advice on the statistical analyses of the data; Dean Shumway for help in analyzing the samples of embryos; and Wayne Klavano for help with the field work.

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Recent Changes in the Walleye Fishery of Northern Green Bay and History of the 1943 Year Class

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ABSTRACT

Production, fishing intensity, and availability of walleyes (*Stizostedion vitreum vitreum*) fluctuated widely in the commercial fishery of northern Green Bay in 1929–57. The catch ranged from 16,000 pounds (8 percent of average for the 1929–53 base period) in 1942 to 1,294,000 pounds (633 percent) in 1950. The index of fishing intensity ranged from 17 (1941) to 400 (1950) and that of abundance from 47 (1929) to 222 (1955). Production and fishing intensity were consistently above average in 1947–57; abundance exceeded the average in 8 of these years. The fishery statistics and records of age and size composition of commercial landings of walleyes in the spring and fall fishing seasons of 1949–58 (scale samples were taken from a total of 1,631 fish) were the basis for a study of recent changes in the walleye fishery with particular reference to the effects of fluctuations in the strength of year classes. The 1943 year class, by a wide margin, exceeded all others in the estimated total number (1,173,000 fish) and weight (3,355,000 pounds) contributed to commercial landings. This year class was a major factor in the sharp rise in production and abundance after 1945 and the all-time record catch of 1950. In contrast, certain other year classes (1945, 1946, 1948) have contributed totals as small as 16,000 to 52,000 pounds. The abundance of the 1950, 1951, and 1952 year classes approached or exceeded that of the 1943 year class at the lesser ages (through the IV group), but these more recent classes disappeared from the fishery so rapidly that their total contributions were relatively low. The indicated increase of mortality in the middle 1950's cannot be attributed to increase in the rate of commercial exploitation. Evidence is offered that the heightened mortality rate resulted from expansion of the sport fishery.

INTRODUCTION

From 1945 to 1957 the walleye (*Stizostedion vitreum vitreum*) fishery of northern Green Bay changed from a small incidental commercial fishery to a major commerical and sport fishery. Hile (1955) has reviewed the recent problems of the fishery and discussed certain controversies which arose. Commercial production of walleyes rose rapidly from 1,000 pounds in 1945 to 1,294,000 pounds in 1950. Commercial fishermen from other parts of the Great Lakes moved to Green Bay to participate in the good fishing, caused extreme competition for good grounds, and created resentment among local fishermen. At the same time, sport-fishing pressure expanded rapidly and extensive resort facilities were built to accommodate the greatly increased numbers of anglers.

Near the height of this expansion various interests sought to restrict the commercial fishery in the hope of preserving the abundant supply of fish. Scale samples taken in the spring of 1949 indicated, however, that the abnormally high abundance of walleyes was caused by a single year class hatched in 1943. Since it was expected that the supply of walleyes would soon decline to a lower level regardless of restrictions on the fishery, most of the proposed restrictions were not adopted. Production and abundance declined drastically in 1951 and 1952, and since the production of the commercial fishery had averaged only 51,000 pounds in 1929–43, it was believed that extremely high abundance probably would not occur again soon. Another peak in abundance was reached in 1955, however, and good fishing continued through 1956.

The purpose of this study is to examine the statistics and age distributions of fish of the commercial fishery for walleyes in Green Bay to obtain information on the contributions of year classes that have passed through the fishery since 1949, especially the 1943 year class. Several people aided in the collection of scale samples. Stanley Lievense of the Michigan Department of Conservation obtained the first scale samples in 1949. Robert Balch, formerly with the Wisconsin Conservation Department, took most of the 1949 and 1950 samples. Leonard S. Joeris and other biologists of the Bureau of Commercial Fisheries took all samples from 1951 through 1958. Several commercial fishermen aided in collection of scales. Ralph Hile offered help in treatment of the data and read the manuscript.

MATERIALS AND METHODS

Scale samples and records of length and weight of walleyes from the commercial fish-

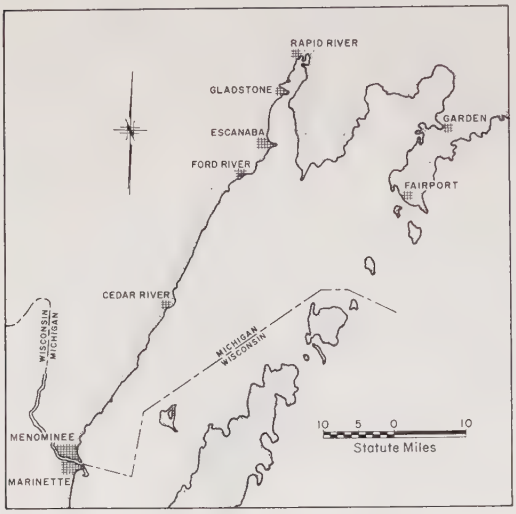

FIGURE 1.—Map of northern Green Bay.

ery were collected by biologists of the States of Wisconsin and Michigan and the U. S. Bureau of Commercial Fisheries. Shortages of personnel and funds prevented thorough coverage of the fishery and left several serious gaps in the data. No coverage of the sport fishery other than general observations was possible. The commercial fishery statistics used are those routinely collected by the State of Michigan and turned over to the Bureau for analysis. Statistical district M-1 encompasses all of the Michigan waters of Green Bay (Figure 1).

Scale samples were taken principally in May and October during the spring and fall peaks of production (Table 1). Spring samples from impounding gear were obtained in all years but one (1952) from 1949 through 1958. Fall samples from these gears were taken in 5 of these 10 years. Three samples were taken from gill nets—September 1949, October 1950, and February 1957. All samples were net-run, but no fish smaller than the legal minimum of 15½ inches, total length, were considered in the present study.

Difficulties in reading the scales were few. Both gelatin mounts and plastic impressions were exceptionally clear. The timing of the collections (spring and fall) eliminated the difficulties of age determination that can be caused by annulus formation, since walleyes grow only in June–September in Green Bay. Throughout this study age refers to the number of annuli. Scales from spring samples were credited with a virtual annulus on the edge of the scale. Although validation of scale reading is not a part of this study, the persistent occurrence of strong and weak year classes in successive years of collection and the presence of some years of exceptionally good and poor growth gave evidence of a high level of accuracy in the reading. Ages were determined for 816 fish from the spring and 472 fish from the fall impounding-gear fisheries, and 343 fish from the gill-net fishery.

Samples from both impounding nets and gill nets were used for estimates of the contributions of age groups and year classes to the commercial production. Samples from gill nets had age distributions that agreed very closely with those taken from impounding nets the same season or were consistent with samples from impounding nets taken in other seasons. No differences could be detected among the various impounding gears. Other gears contributed so little to the total take that even had the age composition of their catches differed from that in impounding and gill nets the estimates based on the catch of major gears still would be valid.

TABLE 1.—*Scale collections from legal-sized walleyes in the commercial fishery of northern Green Bay*

Year and season	Impounding nets	Gill nets	Total
1949			
Spring	109	–	109
Fall	–	171	171
1950			
Spring	57	–	57
Fall	86	72	158
1951			
Spring	46	–	46
Fall	–	–	–
1952			
Spring	–	–	–
Fall	222	–	222
1953			
Spring	37	–	37
Fall	–	–	–
1954			
Spring	70	–	70
Fall	33	–	33
1955			
Spring	47	–	47
Fall	57	–	57
1956			
Spring	141	–	141
Fall	–	–	–
1957			
Spring	158	100	258
Fall	74	–	74
1958			
Spring	151	–	151
Fall	–	–	–
Total			
Spring	816	100	916
Fall	472	243	715
Grand total	1,288	343	1,631

Estimates of the availability of the various age groups in terms of pounds and numbers per unit effort were made from age data for all gears, but statistics on catch per unit effort were for shallow trap nets only. Most of the production from impounding gear came from trap nets during the period of sampling.

The gaps in the sampling schedule (Table 1) made a number of estimates necessary to obtain a continuing sequence of records that could serve as the basis for a coherent account of the fluctuations in the walleye fishery. All estimates are to some degree uncertain, but the range of fluctuation of year-class strength was so great that any errors made were relatively of such minor magnitude that the general conclusions on trends of the fishery are believed to be sound. Rather than interrupt the continuity of later sections with a series of explanations of the assumptions and computational methods, a statement of types of estimates, of procedures followed, and of the basis for the procedures is offered now. References are made to appropriate tables of later sections.

In order to make reasonable estimates of production by year classes from the spring and fall peaks of production, estimates were made of missing age distributions. The estimated age distribution for the spring of 1952 is the same as that of the sample from the fall of the same year except that the III-group was omitted. A comparison of spring and fall samples in other years indicated that, with this omission, the error was small. In no year were III-group fish important in the spring catch.

The age distribution for the fall of 1953 was set up on the assumption that the year-class composition in that season was identical to that in the subsequent spring. Since few age groups were represented in this year, the procedure was believed to be justifiable. The age distribution for the fall of 1956 was computed by averaging the percentage of fish in each year class in the previous and following spring. Since there was no spring sample in 1952, the 1951 fall distribution was computed by averaging the percentages for 1950 and 1952 fall samples in the same manner. Samples taken at several times of the year in 1957 showed that changes in age composition during the year were gradual and progressive in all but age-groups II and III. The averaging of samples of the previous and following years should, therefore, provide a reasonable estimate of age composition. The estimated percentage age compositions (see Table 6 and Figure 3 of a later section) were all consistent with the actual samples.

TABLE 2.—*Average weights of walleyes in spring and fall samples, 1949–57*

Age group	Weight (pounds)	
	Spring	Fall
II	–	1.31
III	1.30	1.46
IV	1.54	2.40
V	1.98	2.98
VI	2.84	3.00
VII	3.11	3.96
VIII	3.13	4.04
IX	4.13	4.37
X	5.69	7.32
XI	6.01	5.86

The weights of age groups employed for the estimation of the numerical and poundage contribution of age groups and year classes to the commercial take were based on the pooled samples (spring and fall separately) of all years' collections. The average weight of fish of the same age and caught in the same season varied somewhat, but without trend, from year to year. Some of this variability may have been caused by annual fluctuations of growth rate, but most of it is believed to result from the small numbers of fish in most samples and the combined effects of sex differences in growth rate and variation of the sex ratio. (Females are much heavier than males of the same age, particularly at the higher ages.) The pooled sample (Table 2), therefore, probably gives a better estimate of the true average weight of an age group in a particular year than does the small sample of the age group taken in that year.

Estimates were made of contributions of the 1943 and 1944 year classes to the fishery in 1946, 1947, and 1948—as early as 3 years before sampling was started (Tables 7 and 8). The tripling of the catch in 1946 over that of 1945 (Table 5) makes it logical to assume that nearly all the 1946 production came from the incoming 1943 year class and that practically all the 1947–48 production came from the 1943 and 1944 year classes. Since in most years fish of age-group III do not come into the catch until fall, the fall production in 1946 and the spring production in 1947 were considered to have come entirely from the 1943 year class. Production from the fall of 1947 and all of 1948 was apportioned between the 1943 and 1944 year classes in the same ratio as their contributions in 1949–53. The low production during the spring of 1946 and the poor representation in

TABLE 3.—*Commercial production (thousands of pounds) of walleyes in northern Green Bay, 1929–57*

Year	Production in gear					Total production
	Pound nets	Shallow trap nets	Fyke and hoop nets	Large-mesh gill nets	Other[1]	
1929	7	7	7	5	1	27
1930	6	5	13	3	—[2]	27
1931	14	5	20	2	1	41
1932	29	8	45	1	2	85
1933	37	18	53	—[2]	1	108
1934	26	17	61	—[2]	4	108
1935	18	11	27	1	—[2]	57
1936	29	17	25	3	—[2]	74
1937	10	17	28	4	—[2]	59
1938	4	9	25	—[2]	—[2]	38
1939	3	6	21	1	—[2]	30
1940	2	8	14	3	—[2]	28
1941	1	10	14	1	—[2]	26
1942	1	4	10	2	—[2]	16
1943	3	12	20	1	—[2]	36
1944	5	17	20	1	—[2]	43
1945	3	12	4	2	—[2]	21
1946	8	50	8	6	1	72
1947	41	148	24	48	1	262
1948	124	229	30	168	21	572
1949	161	421	33	436	12	1,063
1950	99	624	10	560	—[2]	1,294
1951	17	256	8	245	—[2]	525
1952	11	120	11	100	—[2]	242
1953	22	184	9	36	—[2]	252
1954	47	320	2	88	3	460
1955	42	549	—[2]	314	1	906
1956	15	423	—[2]	328	—[2]	766
1957	4	154	—[2]	93	—[2]	251

[1] Includes small-mesh gill nets, hook and line, deep trap nets, trolling, and unknown gear.
[2] Less than 500 pounds.

later samples indicated the 1942 and 1945 year classes were so weak that they could be ignored without significant effect on the estimates of year-class contributions in 1946–48.

Estimates of possible production from the 1951 and 1952 year classes in 1958 and 1959 were included to complete the production histories of the year classes. The ratio of the production of fish of age-groups V and VI from the 1951 year class was applied to the 1952 year class to estimate production at age VI. The regression from age V to VI was extrapolated for both year classes to estimate production at age VII. Estimates of the numerical catch per trap-net lift from these year classes in 1958 and 1959 (Table 10, Figure 5) were based on the assumption that fishing intensity would be the same in these years as in 1957.

Estimates of pounds and numbers have been rounded to the nearest thousand. It is not implied that all figures are correspondingly accurate.

COMMERCIAL FISHERY STATISTICS

The Green Bay walleye fishery is a multiple-gear fishery. Hile, Lunger, and Buettner (1953) have described the seasonal production and types of gear in use prior to 1951. Since 1945 the shallow trap net has been the most important gear in the fishery, but large-mesh gill nets (4½ inches and larger), pound nets, and fyke nets contributed substantially to the total production (Table 3). In 1949 gill nets produced more than any other gear, but since then the trap net has been the major producer. By 1950 the importance of fyke nets was declining, and after 1953 this gear was of little significance. After 1956 pound nets, too, almost disappeared from the walleye fishery.

The methods of handling statistical data on fishing intensity and abundance have been described by Hile (1937), Hile and Jobes (1941), and Van Oosten, Hile, and Jobes (1946). Hile, Lunger, and Buettner (1953) based their estimates of availability or abundance on records of catch per unit effort of pound nets, shallow trap nets, and fyke and hoop nets with 1929–43 as a base period. Their analysis of changes in the Green Bay fisheries extended through 1950. They were most skeptical of the estimates of fishing intensity and abundance for walleyes for the years 1947–50 and commented on the reason for their doubt. The numerous Lake Huron trap-netters who had moved to Green Bay used a larger and much more efficient type of trap net than was fished there prior to World War II. Fishing intensity for later years was, therefore, grossly underestimated, and abundance (ratio of actual catch to expected

TABLE 4.—*Production, fishing intensity, and abundance of walleyes expressed as percentages of the 1929–53 mean*

Year	Production	Fishing intensity	Abundance index
1929	13	36	47
1930	13	34	51
1931	20	34	76
1932	42	50	107
1933	53	38	180
1934	53	41	166
1935	28	38	95
1936	36	45	102
1937	29	40	94
1938	19	47	50
1939	15	40	48
1940	14	23	76
1941	13	17	95
1942	8	17	58
1943	18	21	108
1944	21	19	139
1945	10	27	48
1946	35	76	60
1947	128	170	96
1948	280	260	138
1949	521	396	168
1950	633	400	202
1951	257	270	122
1952	118	198	77
1953	123	164	96
1954	225	184	156
1955	443	256	222
1956	375	245	196
1957	123	119	132

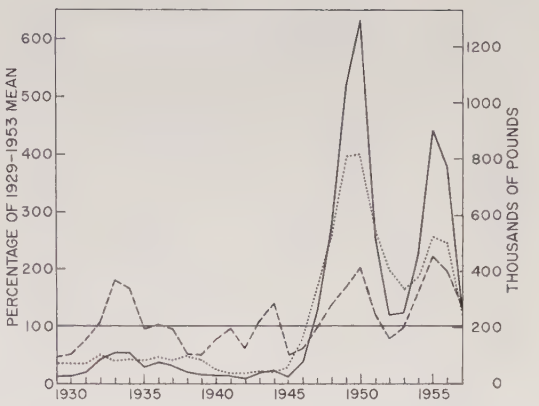

FIGURE 2. — Production (solid line), abundance (long dashes), and fishing intensity (short dashes) in the commercial fishery for walleyes in the State of Michigan waters of Green Bay, 1929–57. Scale at right applies to production; scale at left (percentages of 1929–53 mean) holds for all three variables.

catch) correspondingly overestimated. Inquiries of the local fishermen have since indicated this influx of former Lake Huron operators began as early as 1942 and that by 1945 most of the trap nets were of the larger type. This information made it possible to adjust the average catch per trap-net lift in the 1929–44 and 1945–53 periods according to the average abundance indices obtained from pound and fyke nets during these periods and thus to establish a continuity between the two periods for trap nets. The procedure for making this adjustment was described by Van Oosten, Hile, and Jobes (1946: p. 316). This type of adjustment is subject to some error. Old gears are usually used until worn out and changes in gear, although often rapid, are seldom, if ever, completed in one season. The adjustment permits estimates of intensity and abundance, however, that are far more closely descriptive of the fishery than those made without consideration of changes in gear.

Fishing with gill nets, despite occasional high yields, has not been included in the estimates of abundance. Some question exists as to whether the methods in the gill-net fishery have been stable for a sufficiently long period to establish a dependable base. Until the collapse of the whitefish fishery in 1955, gill nets were fished for whitefish and suckers as well as walleyes, but they are now fished principally for walleyes. Estimates have, therefore, been made from the same gears Hile, Lunger, and Buettner (1953) used, but the indices of intensity cover catches of all gears. The 1929–53 period is used as a base.

Production, fishing intensity, and abundance

Production of walleyes (Tables 3 and 4, Figure 2) in 1929–44 was much lower (generally well below 50 percent of the 1929–53 average of 204,000 pounds) than in the subsequent years. The catches of approximately 108,000 pounds in 1933 and 1934 (53 percent of average) were the highest in the earlier period. The catch fell to only 16,000 pounds (8 percent) in 1942, rose to 43,000 pounds in 1944, then fell again to 21,000 pounds (10 percent) in 1945. A 5-year period of rapidly increasing catch that began in 1946 led to a production of 1,294,000 pounds (633 percent) in 1950. A rapid decline during the next 2 years brought the catch down to 242,000 pounds (118 percent) in 1952. The next 5 years saw another increase to 906,000 pounds (443 percent) in 1955 and another decline to 251,000 pounds (123 percent) in 1957.

Fishing intensity (Table 4, Figure 2) was low throughout the 1929–44 period. It fluctuated between 34 and 50 percent of the 1929–53 average from 1929 through 1939, declined to less than 20 percent in 1941, and remained very low through 1944. An upward trend that began in 1945 ended in 1950 with an index of 400 percent. The intensity index fell to 164 in 1953, rose again to 256 in 1955,

TABLE 5. — *Production of walleyes (thousands of pounds), spring and fall*

Year	Season			Total
	Spring[1]	Fall[2]	Fall expected[3]	
1945	14	6	8	21
1946	15	57	28	72
1947	134	127	102	262
1948	343	229	224	572
1949	563	500	416	1,063
1950	939	355	506	1,294
1951	440	85	205	525
1952	179	63	95	242
1953	123	129	99	252
1954	218	242	180	460
1955	419	486	354	906
1956	618	148	300	766
1957	201	50	98	251

[1] January–July.
[2] August–December.
[3] 39 percent of annual catch (1945–57 average).

then declined to 119 in 1957, the lowest point in 11 years.

Abundance (Table 4, Figure 2), in contrast to production and fishing intensity, was moderately high during the 1929–44 period. Although the index was below 60 percent of average in 1929–30, 1938–39, and 1942, it was above 100 in 6 years and reached the 1929–44 high of 180 in 1933. Abundance was only 48 in 1945 but climbed steadily to 202 in 1950. It declined to 77 in 1952, rose to an all-time high of 222 in 1955, and dropped again to 132 in 1957.

The 1933 peak of production occurred during a time of high abundance and low effort, but the 1949–50 and 1955–56 peaks occurred during periods of high abundance and high effort. In view of the extremely high effort in 1949–50 and the resulting competition for the best grounds, it is possible the efficiency of the gear was not as high as during periods of lower intensity. The true abundance in those years may have been somewhat higher than the index indicates.

Production by season

The calendar year of fishing in Green Bay is divided conveniently into two periods of production. The earlier period runs from January through June and the latter from August through December. July, a month when the fishing is nearly always poor and the catch small, is assigned here to the "spring" production. It is believed that our spring and fall samples are reasonably representative of these periods. Since 1945 production has usually been greater in the spring than in the fall period (Table 5). Fall production averaged 39 percent (unweighted mean of annual percentage) of the annual total in 1945–57.

It appears that the relationship between actual fall production and the "expected" 39 percent of the annual total can be used as a rough index for prediction of production the next spring and the next year. In all years where fall production exceeded the expected percentage, production increased the next spring and *vice versa*. The correlation coefficient between actual deviations from "expected" fall production and changes in spring production the next year was 0.93 ($P < 0.001$). The relationship with production the next entire year is not as close but is good ($r = 0.65$; $p = 0.013$). Higher than "expected" fall production means either continued good take or better production than in the previous year. Lower than "expected" fall production indicates either continued low production or more likely a decline in the catch.

AGE AND YEAR-CLASS COMPOSITION OF THE SAMPLES

The information on age distribution (Table 6, Figure 3) includes actual determinations for available spring and fall samples of walleyes in 1949–58, and an estimate made by procedures described above for each spring or fall when sampling was missed.

The dominance of the 1949 and 1950 samples by the 1943 year class as age-groups VI and VII was extreme. In 1949, 88 percent, and in 1950, 72 percent of the fish sampled were from this year class. This powerful group persisted in the fishery until 1954 (age-group XI) in spite of the high fishing effort in 1948–51. The 1944 year class was small by comparison but remained in the fishery nearly as long as the 1943 fish. The 1945 and 1946 year classes obviously were very weak. The 1947 year class appeared to be moderately plentiful as age-groups III and IV but practically disappeared from the fishery after 1952. During the 1955–56 peak of production, three or four year classes were well represented in the samples in contrast to the one or two in the 1949–50 catch. The fish in the 1949–50 catches belonged principally to age-groups VI and VII, whereas those in the 1955–56 catches were considerably younger.

CONTRIBUTION OF AGE GROUPS AND YEAR CLASSES

To determine the contributions of the various age groups in the different years and seasons, the total weight of each sample was

TABLE 6.—*Percentage age composition in spring and fall samples of walleyes in Green Bay*

[Figures in parentheses are estimates as explained in Materials and Methods]

Age and season	Year of capture									
	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958
I										
Spring	–	–	–	–	–	–	–	–	–	–
Fall	–	–	–	–	–	–	–	–	4	–
II										
Spring	–	–	–	–	–	–	–	4–	2	1
Fall	1–	15	(4)	70	(54)	9	25	(7)	16	–
V										
Spring	–	2	18	(7)	70	54	36	54	10	38+
Fall	2	1	(25)	2	(36)	58–	59–	(63)	14–	–
V										
Spring	4	–	2	(27)	–	36	60–	19	69	16
Fall	16	1	(3)	8	–	24	16	(18)	51	–
VI										
Spring	96	26	2	(5)	–	–	2	19	16	34+
Fall	80	11	–	1	(1)	–	–	(10)	5+	–
VII										
Spring	–	72	13	–	–	1	–	4	–	6
Fall	1	72	(12)	–	–	–	–	(2)	3	–
VIII										
Spring	–	–	65	(10)	3	–	–	–	1	2
Fall	–	–	(56)	3	–	–	–	–	1	–
IX										
Spring	–	–	–	(51)	8	–	–	–	2	1
Fall	–	–	–	16	(3)	–	–	–	–	–
X										
Spring	–	–	–	–	19	3	2	–	–	1
Fall	–	1	–	–	(6)	6	–	–	3	–
XI										
Spring	–	–	–	–	–	6	–	–	–	1
Fall	–	–	–	–	–	3	–	–	3	–
Number in sample										
Spring	109	57	46	–	37	70	47	141	258	151
Fall	171	158	–	222	–	33	57	–	74	–
Average age										
Spring	6.0	6.7	7.1	(7.3)	5.6	5.0	4.8	4.7	5.1	5.3
Fall	5.8	6.3	(6.6)	4.3	(4.0)	4.7	3.9	(4.4)	4.9	–

estimated as the sum of the products, number of fish in each age group times the average weight (grand average weights of Table 2). The ratio of the total commercial production in the season and year to the sample weight then gave a figure for the conversion of numbers and pounds in samples to numbers and pounds in the commercial catch. Determination of the total contribution of each year class required the summation of contributions at different ages and seasons.

The production by age groups (Table 7, Figure 4) illustrates the great strength and persistence of the 1943 year class. Its greatest contribution was at age VII, when nearly a million pounds were produced from this one group. The 1944 year class contributed its greatest poundage at age VI. Later year classes have all contributed their greatest weight at earlier ages (1947, IV; 1949–50, V; 1951–52, IV). The 1943 year class contributed 4.2 times the weight of the 1950 year class, 5.0 times that of the 1952 year class, and more than 200 times that of the weakest year class (1948). More than 3 million pounds were produced from this year class. This production is roughly 15 times the 1929–53 average annual production and 60 times the 1929–43 average, the former base for analysis of the fishery statistics.

The dominance of the 1943 year class over all others is well demonstrated by the percentages of the annual catches made up by each age group. In 1947 more than 90 percent of the production was 1943 fish. As late as 1952, when the year class was at age IX, more than half the catch was still from this group. The highest figure for any other year class is 67 percent for that of 1952 in 1957 (age-group V). No other group has made up more than half the catch at any age.

Numerically, the contribution of the 1943 year class overshadows that of any other (Table 8, Figure 4). Its numerical advantage is,

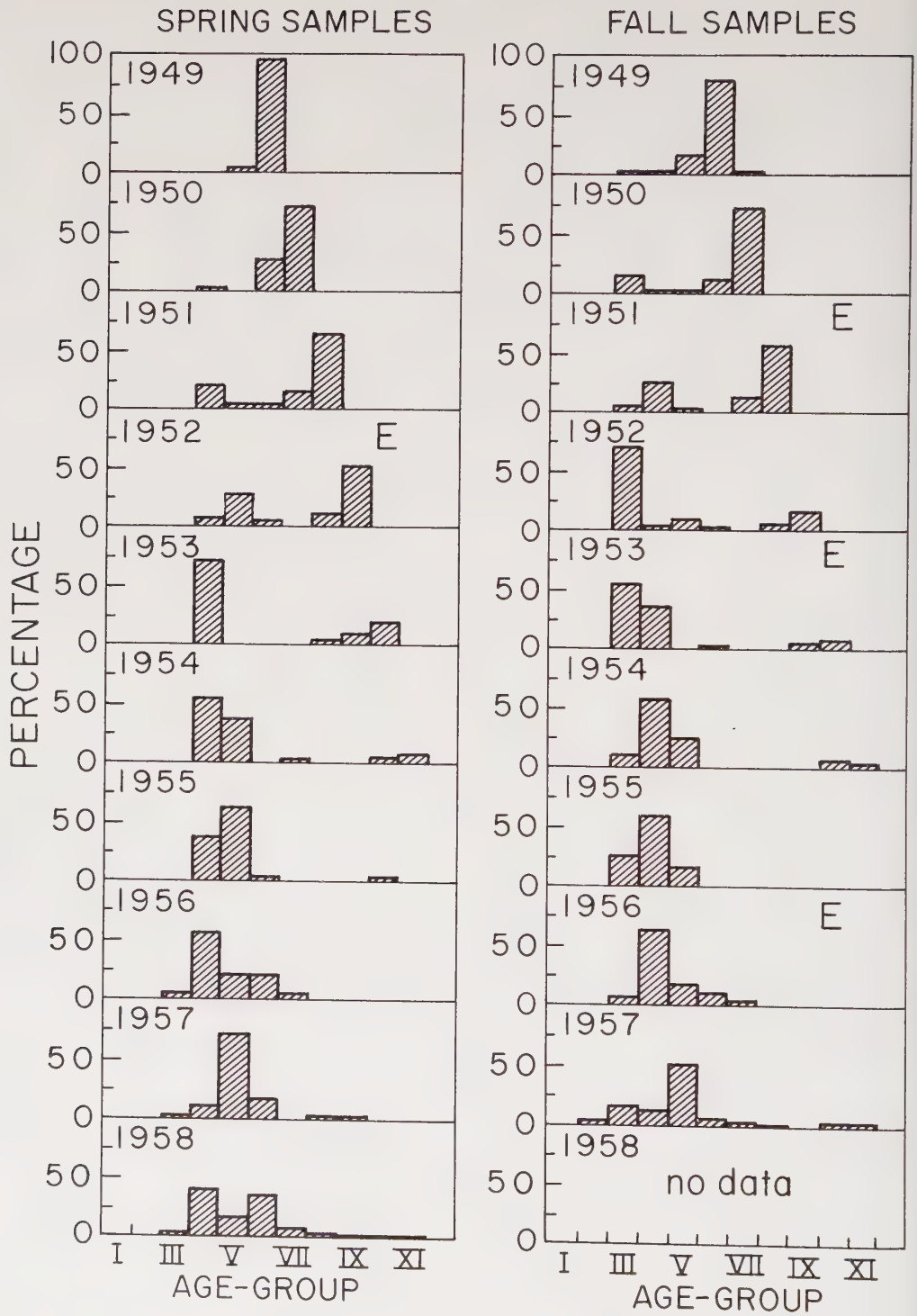

FIGURE 3.—Percentage age composition of spring and fall samples of walleyes in Green Bay. [Graphs marked "E" are estimates.]

TABLE 7.—*Weight contributions (thousands of pounds) to commercial production at each age, and total contributions to the fishery, 1943–1953 year classes of walleyes in northern Green Bay*

[Percentage of total in parentheses]

Year class	Calendar year												Total each year class
	1947[1]	1948[1]	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958[1]	
1943													
Age	IV	V	VI	VII	VIII	IX	X	XI	–	–	–	–	
Pounds	241	480	951	986	374	138	77	51	–	–	–	–	3,355[3]
	(92)	(84)	(89)	(76)	(71)	(57)	(31)	(11)	–	–	–	–	
1944													
Age	III	IV	V	VI	VII	VIII	IX	X	XI	–	–	–	
Pounds	21	92	96	268	75	21	24	54	–	–	–	–	651
	(8)	(16)	(9)	(21)	(14)	(9)	(10)	(12)	–	–	–	–	
1945													
Age	–	–	IV	V	VI	VII	VIII	IX	X	XI	–	–	
Pounds	–	–	7	4	10	–	4	–	27	–	–	–	52
	–	–	(1)	–[2]	(2)	–	(2)	–	(3)	–	–	–	
1946													
Age	–	–	III	IV	V	VI	VII	VIII	IX	X	XI	–	
Pounds	–	–	1	10	9	9	–	–	–	–	5	–	34
	–	–	–[2]	(1)	(2)	(4)	–	–	–	–	(2)	–	
1947													
Age	–	–	–	III	IV	V	VI	VII	VIII	IX	X	–	
Pounds	–	–	–	22	56	37	2	5	–	–	3	–	125
	–	–	–	(2)	(11)	(15)	(1)	(1)	–	–	(1)	–	
1948													
Age	–	–	–	–	III	IV	V	VI	VII	VIII	IX	–	
Pounds	–	–	–	–	1	8	–	–	–	–	7	–	16
	–	–	–	–	–[2]	(3)	–	–	–	–	(3)	–	
1949													
Age	–	–	–	–	–	III	IV	V	VI	VII	VIII	–	
Pounds	–	–	–	–	–	29	101	135	13	47	2	–	327
	–	–	–	–	–	(12)	(40)	(29)	(1)	(6)	(1)	–	
1950													
Age	–	–	–	–	–	–	III	IV	V	VI	VII	–	
Pounds	–	–	–	–	–	–	45	204	359	192	4	–	804
	–	–	–	–	–	–	(18)	(44)	(40)	(25)	(2)	–	
1951													
Age	–	–	–	–	–	–	–	III	IV	V	VI	VII	
Pounds	–	–	–	–	–	–	–	11	430	153	48	15	657
	–	–	–	–	–	–	–	(2)	(47)	(20)	(19)	–	
1952													
Age	–	–	–	–	–	–	–	–	III	IV	V	VI	
Pounds	–	–	–	–	–	–	–	–	77	354	167	52	666[4]
	–	–	–	–	–	–	–	–	(8)	(46)	(67)	–	
1953													
Age	–	–	–	–	–	–	–	–	–	III	IV	–	
Pounds	–	–	–	–	–	–	–	–	–	21	7	–	—
	–	–	–	–	–	–	–	–	–	(3)	(3)	–	
Total annual production	262	572	1,063	1,294	525	242	252	460	906	766	251	–	—

[1] Estimates, explained in text.
[2] Less than 0.5 percent.
[3] Includes an estimated 57,000 pounds taken at age III in 1946.
[4] Includes an estimated 16,000 pounds taken at age VII in 1959.

however, not as great as its production advantage. Its numerical contribution was 3.2 times that of both the 1950 and 1952 year classes in contrast to 4.2 and 5.0 times, respectively, for the poundage contribution. The greatest numerical contributions from the 1943 and 1944 year classes were at age VI. The 1949 and 1950 year classes contributed most at age V and the 1951 and 1952 year classes at age IV.

The 1948–51 peak of production was supported almost entirely by the 1943 and 1944 year classes. Prior to 1951, more than 75 percent of the numerical catch was 1943 fish. The reduced production of 1952–54 was caused by the extreme weakness of the 1945, 1946, and 1948 year classes. The 1954–56 peak of production was sustained by four (1949 through 1952) year classes. Of the 1955 catch, 48 percent came from the 1951 year class and of the 1956 catch, 55 percent was from the 1952 year class. Because of the early disappearance of recent year classes from the fishery, only the 1952 year class contributed heavily (75 percent of the catch) in 1957, and, consequently, total production fell drastically (Table 3).

The average weight and age of a year class

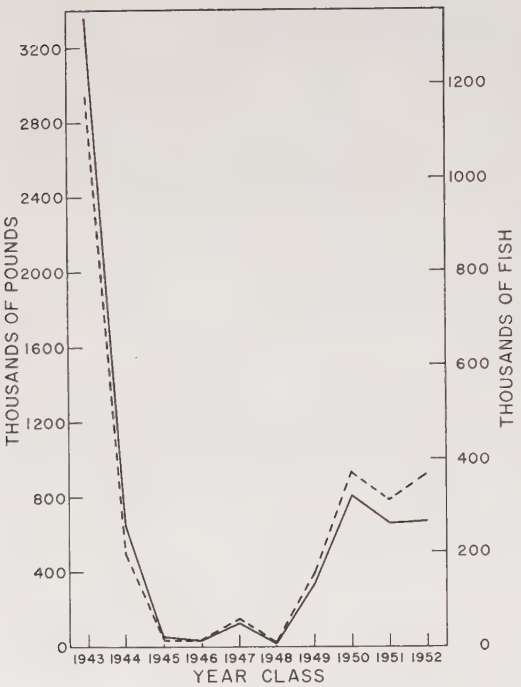

FIGURE 4.—Contributions to the fishery by the year classes of 1943 through 1952. Solid line, pounds; broken line, number of fish.

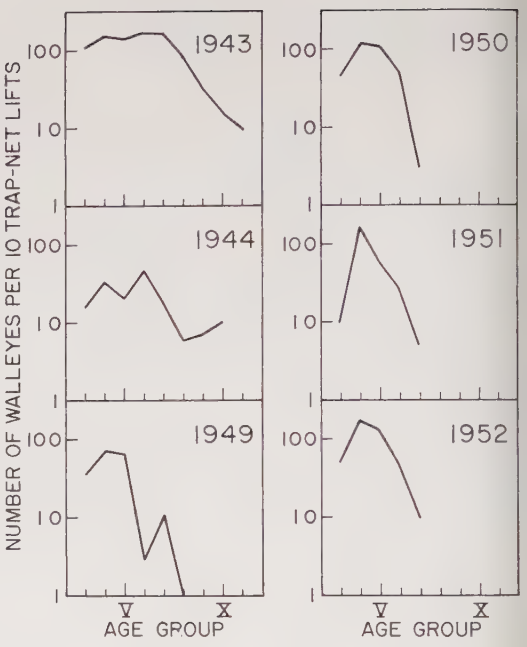

FIGURE 5.—Catch curves (number per unit effort on a log scale) of certain year classes of walleyes in northern Green Bay.

at capture (Table 9) have declined considerably during the years covered by this paper. The year classes of 1949 through 1952 averaged from 0.7 to 1.0 pound less at capture than the 1943 year class. The 1952 year class appears to have averaged less than two-thirds the weight of the 1943 year class at capture. This decrease in average weight is a direct consequence of the decrease in average age. Average age at capture of the 1943 year class was 1.4 to 2.4 years greater than that of the 1949–1952 year classes. The 1944 year class also averaged considerably heavier and older than more recent year classes.

ABUNDANCE OF AGE GROUPS AND YEAR CLASSES

The fluctuations in effort have been great enough since 1946 so that production summations are not a satisfactory index to strengths of year classes. Results of comparisons of year-class strength based on production summations (numbers of fish) can be affected greatly by the nature of the fluctuations of effort. If two equal-sized year classes are subjected to different or varying fishing rates, the one subjected to the greater effort during the years most closely following the age of significant or complete vulnerability will appear the larger of the two. High natural mortality intensifies this effect since more fish die of natural causes in groups where fishing mortality is low in earlier years.

Data on the numbers of walleyes of various age groups taken per unit of fishing effort provide a somewhat better basis for comparisons of year-class strength than do the summations of total numbers, but even these records offer certain troublesome problems of interpretation. If, for example, a year class enters the fishery during a period of intensive exploitation, its members may be cropped off so rapidly as they attain the 15½-inch minimum size that most have been taken well before the year class attains full vulnerability.[1] The catch per unit effort of the year class can be expected to decrease sharply soon after it

[1] The matter of vulnerability to the gear is of little consequence in this discussion since the principal impounding gears — trap nets, fyke nets, and the great majority of pound nets — have meshes small enough to hold any walleye of legal length. Large-mesh gill nets may not hold all 15½-inch walleyes, but the good agreement of age distributions in samples from gill nets and impounding nets suggests that escapage was small. Vulnerability is, therefore, used here to indicate attainment of legal size.

TABLE 8.—*Contributions to the commercial fishery (thousands of fish) at each age and total numerical contributions to the fishery by the 1943–1952 year classes of walleyes in northern Green Bay*

[Percentage of total in parentheses]

Year class	Calendar year												Total each year class
	1947[1]	1948[1]	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958[1]	
1943													
Age	IV	V	VI	VII	VIII	IX	X	XI	–	–	–	–	
Number	132	209	327	297	115	33	12	9	–	–	–	–	1,173[3]
	(90)	(80)	(89)	(79)	(64)	(39)	(11)	(5)	–	–	–	–	
1944													
Age	III	IV	V	VI	VII	VIII	IX	X	XI	–	–	–	
Number	14	51	35	58	23	7	6	8	–	–	–	–	202
	(10)	(20)	(10)	(15)	(13)	(8)	(6)	(4)	–	–	–	–	
1945													
Age	–	–	IV	V	VI	VII	VIII	IX	X	XI	–	–	
Number	–	–	3	1	3	–	1	–	5	–	–	–	13
	–	–	(1)	–	(2)	–	(1)	–	(1)	–	–	–	
1946													
Age	–	–	III	IV	V	VI	VII	VIII	IX	X	XI	–	
Number	–	–	1	6	4	3	–	–	–	–	1	–	15
	–	–	–	(2)	(2)	(3)	–	–	–	–	(1)	–	
1947													
Age	–	–	–	III	IV	V	VI	VII	VIII	IX	X	–	
Number	–	–	–	15	33	17	1	1	–	–	–[2]	–	67
	–	–	–	(4)	(18)	(20)	(1)	(1)	–	–	–	–	
1948													
Age	–	–	–	–	III	IV	V	VI	VII	VIII	IX	–	
Number	–	–	–	–	1	5	–	–	–	–	2	–	8
	–	–	–	–	(1)	(6)	–	–	–	–	(2)	–	
1949													
Age	–	–	–	–	–	III	IV	V	VI	VII	VIII	–	
Number	–	–	–	–	–	20	54	58	5	15	1	–	153
	–	–	–	–	–	(24)	(51)	(31)	(1)	(4)	(1)	–	
1950													
Age	–	–	–	–	–	–	III	IV	V	VI	VII	–	
Number	–	–	–	–	–	–	31	105	164	67	1	–	368
	–	–	–	–	–	–	(30)	(55)	(38)	(18)	(1)	–	
1951													
Age	–	–	–	–	–	–	–	III	IV	V	VI	VII	
Number	–	–	–	–	–	–	–	8	207	72	17	5	309
	–	–	–	–	–	–	–	(4)	(48)	(19)	(16)	–	
1952													
Age	–	–	–	–	–	–	–	–	III	IV	V	VI	
Number	–	–	–	–	–	–	–	–	53	209	80	18	365[4]
	–	–	–	–	–	–	–	–	(12)	(55)	(75)	–	
1953													
Age	–	–	–	–	–	–	–	–	–	III	IV	–	
Number	–	–	–	–	–	–	–	–	–	15	4	–	—
	–	–	–	–	–	–	–	–	–	(4)	(4)	–	
Total annual production	146	260	366	377	179	85	105	189	434	378	106	–	—

[1] Estimates, explained in text.
[2] Fewer than 500 fish.
[3] Includes an estimated 39,000 fish taken at age III in 1946.
[4] Includes an estimated 5,000 fish taken at age VII in 1959.

first appears in the commercial landings. A year class that is fished lightly, on the other hand, may show an increase of numbers per unit effort over several years — as long as recruitment through attainment of legal size exceeds losses through fishing and natural mortality. We lack good information to judge the rate of attainment of legal size by Green Bay walleyes. Instructive, though not directly applicable, information on this point is given by the length–frequency data published by Hile (1954) for net-run samples of Saginaw Bay walleyes captured by small-mesh impounding nets in 1926–30. According to his records an occasional fish reached 15½ inches in three growing seasons but some females were still undersized at the end of five seasons and some males at the end of seven. Smith and Pycha (1961) also presented data on an extended period of recruitment in the gill-net fishery for walleyes in the Red Lakes, Minnesota. If the length of time between first and full vulnerability is equally large for Green Bay walleyes, interpretation of data on catch per unit effort of various age groups is uncertain to some degree.

TABLE 9.—*Average weight (pounds) and age (mean number of annuli) at capture of the 1943–1952 year classes*

Year class	Average weight	Average age
1943	2.86	6.1
1944	3.22	5.5
1945	4.00	7.2
1946	2.27	5.1
1947	1.86	4.1
1948	2.00	5.1
1949	2.14	4.6
1950	2.18	4.7
1951	2.13	4.4
1952	1.82	3.7

The first step in estimating the abundance of walleyes of different year classes at various ages required the use of sample data and records of trap-net production to calculate the numbers of walleyes of each age produced by trap nets in the spring and fall season of each year (see "Materials and Methods" for details of the procedure). Once the total for an entire year (sum of spring and fall estimates) was determined, the records of the annual number of trap-net lifts permitted computation of the number taken per lift for each age group. Since these numbers were sometimes small, the records of Table 10 are in terms of 10 trap-net lifts (Figure 5).

Fish of age-group III are, obviously, not fully vulnerable. Other age groups of the various year classes exhibit differences and trends that cannot be explained from the commercial fishery statistics. The slope of the survival curve for the 1943 year class indicates this group may not have been fully vulnerable until age VII or VIII although it entered the fishery as age-group III. Its maximum availability was as age-group VI or VII. The 1944 year class was most available as age-group VI. The 1949–1952 year classes were all most available as age-group IV although full vulnerability was undoubtedly at a later age for most of these year classes. The 1943 fish were still being caught in significant numbers at age X and XI, but the 1949–1952 year classes had all but disappeared by age VIII.

The early disappearance from the fishery and lower age of maximum availability of year classes more recent than that of 1946 points clearly to an increased total mortality among the later groups. Evidence is lacking for an increased natural mortality. Hile and Buettner (1959) gave evidence for their belief that the sea lamprey was the principal cause of the decline of the Saginaw Bay walleye in the middle and late 1940's. The situations in Saginaw Bay and Green Bay are, however, dissimilar. The decline of the walleye in Saginaw Bay followed closely the decline of the lake trout in Lake Huron. In Green Bay the abundance of walleyes was very high at the time the lake trout fishery had almost completely collapsed.

Neither can the increased mortality of the more recent year classes be traced to commercial operations. Fishing intensity (Table 4) has not increased but, on the contrary, has decreased. Fishing intensity was so high in 1948–51 (average index 331) as compared to 1954–57 (average index 201) that an increase, rather than a decrease, of average age and age of maximum availability would have been expected. A major increase in efficiency of the gear in recent years cannot properly be postulated as the cause of increased mortality. As was mentioned in an earlier section, the gear has not changed appreciably since 1946.

A marked increase in growth rate might account for recruitment at an earlier age, but not for an increase in fishing mortality after the fish have reached vulnerability. Evidence of a significant change in growth rate is lacking, however. Fish of the 1943–1944 year classes were nearly as heavy at corresponding

TABLE 10.—*Number of walleyes from each year class (1943–1952) taken per 10 trap-net lifts at each age*

Age	Year class									
	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
III	111[1]	16[1]	–[1]	1	12	1	36	47	10	52
IV	154[1]	34[1]	2	3	27	4	71	124	173	177
V	141[1]	21	1	3	17	–	66	111	59	132
VI	168	48	2	3	1	–	3	52	27	46[1]
VII	166	18	–	–	2	–	11	3	5[1]	10[1]
VIII	87	6	2	–	–	–	1	–	–	–
IX	32	7	–	–	–	2	–	–	–	–
X	16	10	3	–	1	–	–	–	–	–
XI	10	–	–	2	–	–	–	–	–	–
Total	885	160	10	12	60	7	188	337	274	417

[1] Estimates; explained in "Materials and Methods."

ges as were those from the 1949–1952 year lasses.

The sport fishery, on the other hand, is definitely known to have contributed to increased walleye mortality. The sport fishery developed mainly in response to the increase in abundance caused by the 1943 year class. In 1948 and 1949 angling was so good that many local anglers took out commercial licenses. In 1948 these "commercial" anglers averaged 60 pounds of walleyes per day and produced a total of 20,000 pounds. These figures represent only a small fraction of the sport-fishery production but offer good indication of the excellent quality of the fishing. The resort, dock, and boating facilities have been expanding so rapidly that even in the early and middle 1950's the scale of fishing must have been very large.

The first indication of the truly great magnitude of sport fishing for walleyes in Green Bay came from Eschmeyer's[2] report on a walleye tagging study initiated in September 1957 in northern Green Bay. The percentage return was low (a total of only 11.6 percent after two fishing seasons) as might be expected when a reward is not offered, but the comparative returns from anglers and commercial fishermen are pertinent to this study. Of 282 returns, 209 (74.1 percent) were from anglers and only 73 (25.9 percent) were from commercial operators. There is no reason to believe that one group of fishermen was more cooperative than the other in the return of tags. The lower returns from commercial operators are believed, therefore, to provide sound evidence that the sport fishermen took approximately three times as many tagged walleyes in 1958–59 as did commercial fishermen. The evidence suggests strongly, then, that the increase in mortality in recent years can be attributed to an increase in the intensity of the sport fishery.

The indication that the increase in mortality was caused by an increase in sport fishing further complicates the problem of estimating relative year-class strengths. Since the size limit for anglers is only 13 inches as against 15½ inches for commercial fishermen, a year class can suffer considerable reduction before it first becomes available to the commercial fishery. We therefore have no truly discriminating method for comparing the strength of year classes that were in the fishery during the early years of sampling with that of the more recent year classes. The problem, then, is finding the procedure that is least biased.

Table 11.—*Catch of walleyes of 10 year classes at age IV per unit effort of 10 trap-net lifts*

[Expressed as numbers of fish and as percentage of the 10-year average]

Year class	Number at age IV per unit effort	Percentage of average
1943	154	201
1944	34	44
1945	2	3
1946	3	4
1947	27	35
1948	4	5
1949	71	92
1950	124	161
1951	173	225
1952	177	230

Smith and Pycha (1961) used summations of the catch per unit effort at each age for an index to the strength of a year class. Their problem was to overcome differences in vulnerability to the gear at any one age caused by large annual fluctuations in growth rate. This procedure is of little use in a situation where total mortality has varied greatly as it has in northern Green Bay.

Under the circumstances that have been outlined, the best estimate of relative year-class strengths is probably made from a comparison of the numerical catches per unit effort of walleye at age-group IV, the earliest age at which most of the year classes had a substantial number of fish available to the commercial fishery. Even with this limitation the lower size limit for anglers will tend to make the estimates of the relative strength of the more recent year classes low. Annual fluctuations in growth rate could have affected the number of fish available at age IV in any year. Even though, as was explained earlier, we have no evidence of a truly large change of growth rate, the effects of small changes could have been material. To add further to the uncertainty are the small sizes of some samples and the fact that the numbers of IV-group fish of the 1943 and 1944 year classes are based on estimates. Estimates of relative year-class strength based on age-group IV fish (Table 11) accordingly must be viewed with some skepticism and interpreted with caution.

Despite the shortcomings of the data, the records of Table 11 do permit some definite conclusions. It is clear that the fluctuations of year-class strength of Green Bay walleyes

[2] Eschmeyer, Paul H. (1959) Great Lakes fishery research by the Michigan Department of Conservation, 1959. Report to the Upper Great Lakes Fishery Committee, Annual Meeting. (Multigraphed.)

have been enormous (well over fiftyfold). It is also clear that the original strength of such recent year classes as those of 1951 and 1952 matched or probably exceeded the strength of the extremely productive 1943 year class. The failure of recent strong year classes to attain their potential commercial productivity can be attributed to a fishing rate so high that they were eliminated at an early age and, hence, at a relatively small size.

IMPLICATIONS FOR FUTURE MANAGEMENT

The wide range of variability of year-class strength and the considerable number of years that may separate the appearance of strong year classes suggest that wide fluctuations of abundance and production will continue to characterize the walleye fishery of northern Green Bay. The effects of this variability have been heightened in recent years by an increase of fishing mortality that eliminates each incoming year class at an early age.

Any attempt to stabilize abundance and production by spreading the exploitation of a year class over a longer period of years must be based on a lowering of fishing mortality. Inasmuch as evidence now available indicates that the increase of mortality came about through a great expansion of sport fishing and that anglers take many more walleyes than do commercial fishermen, we must look principally toward regulations of angling if any substantial reduction in fishing mortality is to come about. Relatively little can be gained from further restrictions on the already stringently regulated commercial fishery.

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SHORT PAPERS AND NOTES

Movement of Tagged Halibut off New England—II

Since our previous report (Wise and Jensen, 1959), we have tagged 11 more Atlantic halibut, *Hippoglossus hippoglossus* (Linnaeus), and have received reports of 17 recaptures, for a total of 34. Two of the 17 were from the 11 recently tagged and 13 from experiments conducted in 1957. Unfortunately, two had lost the numbered discs when captured, although we suspect that one of these was tagged on Grand Manan Banks in October or November 1957.

Fish in the recent tagging operations were captured in an otter trawl and marked as follows:

Date	*Place*	*Number tagged*	*Length in centimeters*
April 1959	Browns Bank	5	38–51
	Jeffreys Ledge	3	30–56
March 1960	Browns Bank	3	46–59

One of the Browns Bank fish marked in 1959 and all of the Jeffreys Ledge fish were released with Lea tags anchored internally. The rest of the 1959 halibut were marked with plastic spaghetti tags. All of the 1960 halibut were released with Petersen discs secured on stainless steel wire through the dorsal musculature.

Two fish from the 1957 taggings, recaptured since the last report, were taken a very few miles from where they had been released, although they had been at large 80 and 109 weeks, respectively. One had been tagged on Browns Bank and one on Grand Manan Bank. Two other returns, a fish at large 156 weeks from the same operation, and one from the 1960 tagging out for only 5 weeks, had insufficient information about recapture location.

The 11 halibut whose movements are shown in Figure 1 were all tagged on Browns Bank. Four were recaptured on or near the Grand Bank, at least 600 nautical miles from Browns Bank, from 103 to 128 weeks after they were released. Five were caught well to the eastward on the Nova Scotian Banks, from 200 to nearly 500 miles from Browns, 50 to 113 weeks after release. Two were caught less than 100 miles from Browns Bank after being at large 113 and 128 weeks. These results are

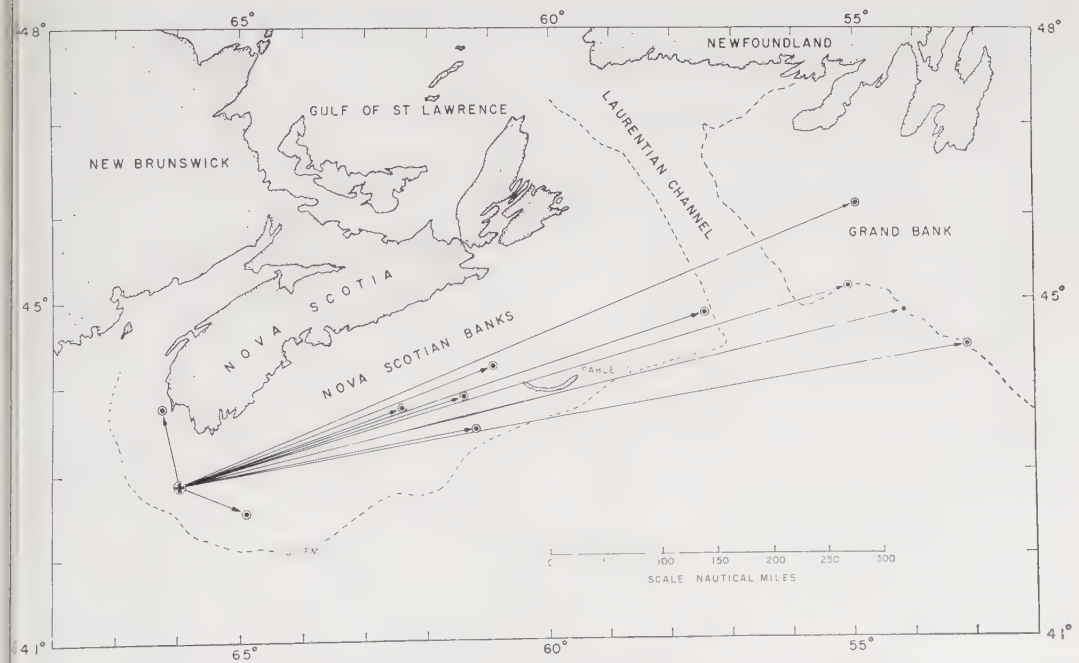

FIGURE 1.—Movements of halibut tagged on Browns Bank and recaptured after 50 or more weeks at large.

quite similar to those reported by McCracken (1958) from his tagging in western Nova Scotian waters in 1947, except that far fewer of his fish in number or percentage moved long distances or crossed the Laurentian Channel.

The mean length at tagging of the fish which went to the Grand Bank was 55 centimeters, of the fish which moved along the Nova Scotian Banks 45 centimeters. The mean length at tagging of the four fish which traveled relatively short distances (including the two not shown because of the scale of the figure) was 57 centimeters. This does not bear out the suggestion in our previous work that it is the larger fish which move the longer distances.

The previous conclusions about the superiority of the Lea tag for halibut still hold, since these tags used at various times and places have yielded about 28 percent returns in contrast to about 16 percent for other types, even though at the time of this writing some of the Lea tags have been out only just over a year. In addition, several letters which accompanied returned tags mentioned that the Petersen discs had become imbedded in the flesh, presumably as the fish grew, and in one case at least discovery of the tag was prevented until the fish was being cut up in a retail market, with consequent loss of information. Three of the Petersen discs have been returned with the numbered member of the pair missing, which contributed to scanty information.

In summary, since the beginning of our halibut work in 1956, 202 halibut have been tagged in the waters off New England. Thirty-four, about 17 percent, of these have been reported as recaptured. While some small numbers of halibut marked at other places have yielded larger percentages, the 79 (erroneously reported before as 78) tagged on Browns Bank in the spring of 1957 and the 68 tagged there in the fall of the same year, with 14 and 7 returns respectively, have yielded the most information about migrations of halibut, particularly long distance movements.

It is difficult to draw any definite conclusions as to movements of halibut from these results. Bigelow and Schroeder (1953) point out the contradictory nature of evidence bearing on halibut migrations in the Gulf of Maine and in Nova Scotian waters. Our present results disagree somewhat with our own previous conclusion that it is the larger fish which migrate and with Martin and McCracken's (1950) finding that halibut do not cross the deep Fundian and Laurentian Channels. It should be pointed out that in a re-examination of the data augmented by more returns McCracken (1958) found that one fish had gone from Browns Bank to the Grand Bank and one from the Gulf of St. Lawrence to Iceland.

Thus halibut of medium size or larger are capable of and do perform long migrations in the Northwest Atlantic, but whether the individual fish moves or not seems almost a matter of chance.

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Use of a Fishwheel in Salmon Research and Management

For many years fishwheels have been used throughout the west coast of the United States and Canada as a type of gear for the commercial and subsistence harvest of anadromous fishes. Fishwheels were originally developed for commercial use on the Columbia River and have been used commonly by the Indians of the Yukon and Kuskokwim Rivers in Alaska. In 1951 biologists of the Alaska Department of Fisheries[1] developed plans and constructed a fishwheel to determine the effectiveness of this gear for measuring the escapement of salmon runs in Alaska. While the investigation was primarily concerned with chinook salmon (*Oncorhynchus tshawytscha*), it was expanded to include observations on the sockeye salmon (*O. nerka*), pink

[1] Now the Alaska Department of Fish and Game.

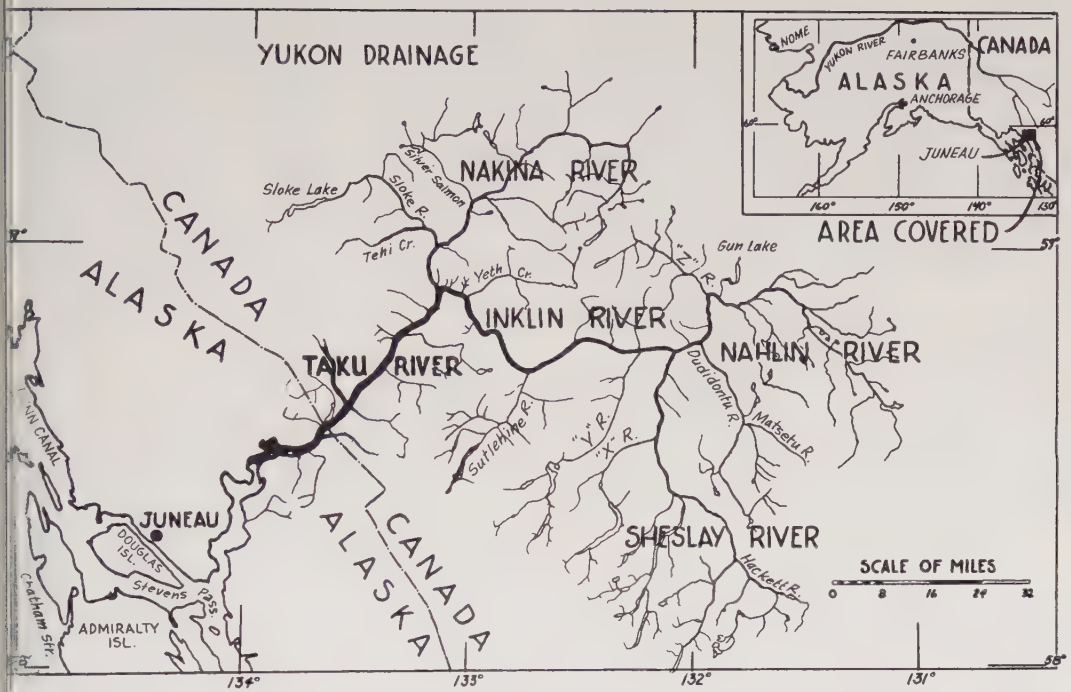

FIGURE 1.—Map of Taku River watershed and waters adjacent to its mouth.

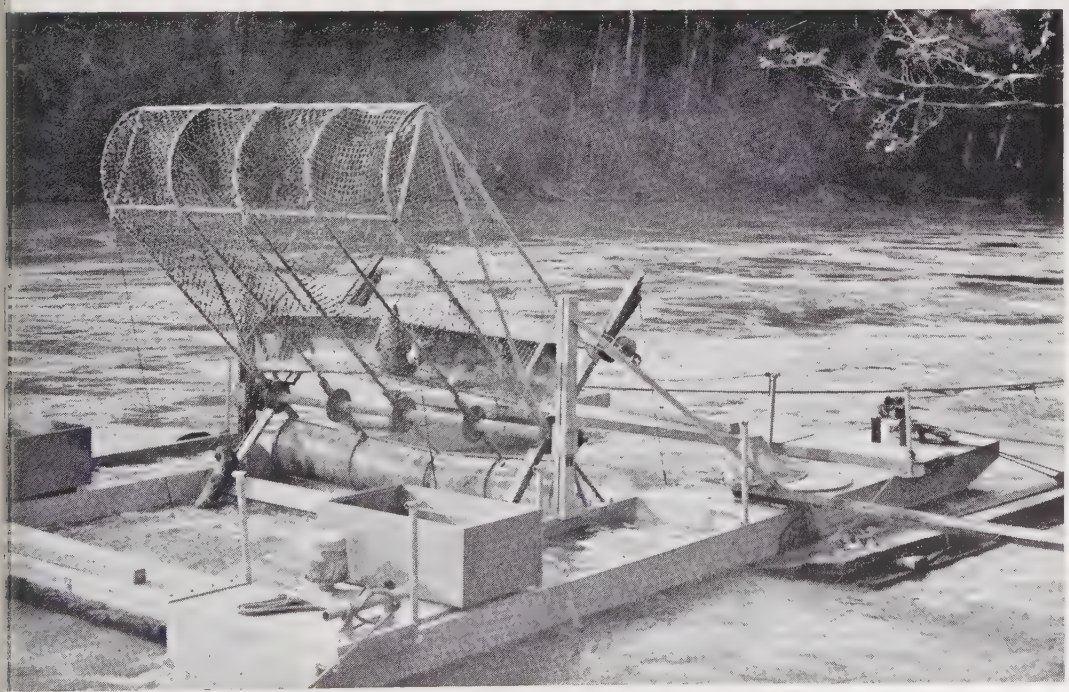

FIGURE 2.—Taku River fishwheel.

TABLE 1.—*Average fork length in centimeters of Taku salmon, 1958 and 1959, at fishwheel and at the Nakina River spawning site*

Sex	Year	Fishwheel	Spawning site	Mean difference	Significance[1] (t)
Male	1958	48.92 ($N = 410$)	54.18 ($N = 4,423$)	5.26	5.62
	1959	55.58 ($N = 1,502$)	62.61 ($N = 1,202$)	7.03	10.61
Female	1958	75.70	87.09	11.39	11.77
	1959	89.08 ($N = 537$)	90.17 ($N = 2,890$)	1.09	3.27
Total combined sexes	1958	53.06 ($N = 485$)	58.36 ($N = 5,067$)	5.30	5.42
	1959	64.32 ($N = 2,039$)	70.69 ($N = 4,092$)	6.37	10.38

[1] All differences significant at the 1-percent level.

salmon (*O. gorbuscha*), coho salmon (*O. kisutch*), and chum salmon (*O. keta*).

DESCRIPTION OF STUDY AREA

The area chosen for this investigation was the Taku River, a turbid glacial river typical of many of Alaska's salmon streams. The Taku originates in the high plateau country of northwestern British Columbia (Figure 1). It is largely of glacial origin but has two major clear-water tributaries, the Nakina and the Nahlin (Kerr, 1948). Extensive aerial and foot surveys of the watershed have shown that the bulk of chinook salmon spawning occurs in these two rivers with the Nakina accounting for the largest share. The Taku empties into Taku Inlet about 30 miles south of Juneau. A gill-net fishery has operated in Taku Inlet for approximately 65 years with an increasing number of boats in recent years. In 1960 approximately 80 boats were operated. The study site was at Canyon Island, located about 14 miles up-river from its mouth. This stretch is the narrowest part of the lower river and provides a natural "funnel" through which fish moving upstream must pass.

THE FISHWHEEL

The Taku River fishwheel (Figure 2) consists of a pontoon framework supporting two scoop-like baskets which are turned by the force of the current against two paddle-like wings set at right angles to the scoops. Originally the scoops were fitted with cotton and then nylon netting, but finally with 1½-inch-square wire mesh. The latter was more effective, more durable, and fish did not have the tendency to hang up in it which they did when netting was used. A fish is picked up by one of the scoops, then drops onto a slide which guides the fish into one of the live wells built into each pontoon. A short section of stovepipe (with a 90° elbow on one end and

TABLE 2.—*Recaptures of all species of tagged salmon by fishwheel, 1958–59*

Species	Year	Number caught	Number tagged	Number recaptured[1]	Percentage recaptured
Chinook	1958	488	473	2	0.42
	1959	2,039	1,708	26	1.52
Sockeye	1958	258	241	8	3.32
	1959	359	342	3	0.88
Pink	1958	2,811	1,024	81	7.91
	1959	12,371	1,081	90	8.33
Chum	1958	1,300	599	13	2.17
	1959	642	610	11	1.80
Coho	1958	187	74	0	0
	1959	619	591	4	0.68
All species	1958	5,044	2,411	104	4.31
	1959	16,031	4,332	134	3.09

[1] Number recaptured is considered in number tagged, *i.e.*, a fish captured twice is considered as two tagged fish.

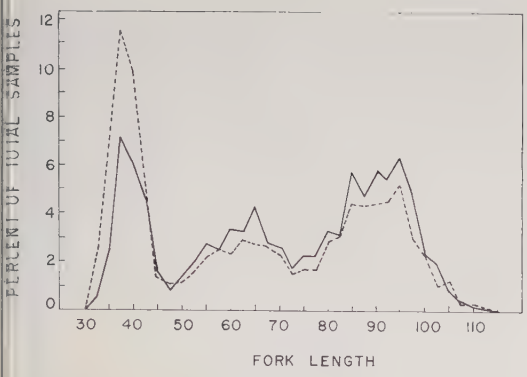

FIGURE 3. — Fork-length frequencies in 2.5-centimeter groups of chinook salmon taken by fishwheel and on Nakina spawning grounds—1959. Solid line, 1,088 fish on spawning grounds; dashed line, 2,035 fish at fishwheel.

covered by a perforated cap on the other end) is attached to each paddle assembly and delivers fresh water to the live wells with each revolution of the wheel. Boards may be added to or removed from the paddle assembly to vary the speed of revolution in order to keep the wheel turning over at a constant rate. It was found to be most effective when operating at about 4 revolutions per minute.

EXPERIMENTAL PROCEDURE

The fishwheel was put into operation as soon as possible each spring and fished 24 hours a day. All chinook salmon were tagged with Petersen disc tags. During the last 2 years of the study (1958 and 1959) fish were anesthetized with tricaine methanesulfonate (MS-222) prior to tagging and then transported by a river skiff equipped with a live box to a quiet-water slough about 1 mile below the tagging site. Here the fish were released where they could recover from the effects of the anesthetic before again venturing into the swift current of the main river. Similar methods were used to tag and release the other four species of salmon taken in the wheel. This procedure afforded an opportunity to determine the rate of recapture of tagged fish.

During late July and August each year from 1956 through 1959, a carcass-collecting weir was constructed immediately below a 2-mile spawning area on the Nakina River, about 15 miles above its confluence with the Taku and approximately 50 miles above the Canyon Island tagging site. Carcasses were collected from the weir twice a day, and every

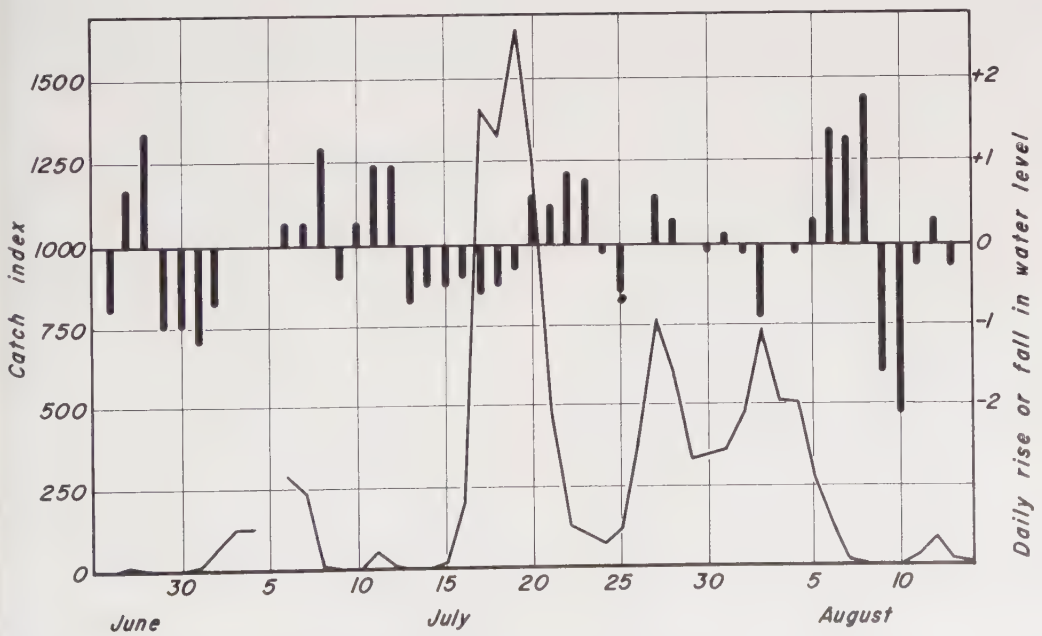

FIGURE 4.—The daily fishwheel catch of pink salmon compared to the daily rise or fall in the water level at Canyon Island.

other day a foot survey was made of the 2-mile spawning stretch in order to retrieve the carcasses which had lodged among the rocks and alders and those which had been dragged by bears onto the shore and bars (Meehan, 1961). The fork length and eye length (posterior rim of orbit to fork of tail) of each fish were recorded; then each fish was opened to check sex, spawning success of females, and to supply a distinctive mark so that no carcasses would be counted again on subsequent days. Tag numbers of fish which had been tagged at the Canyon Island Station earlier in the year were recorded. Using the tagged fish as a basis, a conversion table was designed which eliminated errors due to increase in length of fish between the tagging site and the spawning grounds from the development of secondary sex characteristics (elongated jaws, etc.).

RESULTS AND DISCUSSION

In each of the 4 years that the carcass weir was installed (1956–59), it was demonstrated that the fishwheel was more efficient in capturing the smaller chinook salmon than it was in capturing the larger chinooks. This bias is shown by Table 1 for the years 1958 and 1959 and by Figure 3 for 1959. These 2 years were chosen as examples because the fishwheel was fished at Canyon Island in the same location in these years. During 1956 and 1957 it was moved several times in an attempt to establish a more efficient sampling site. Assuming that the spawning population on the Nakina is representative of the entire Taku chinook salmon run, the fishwheel is biased in that it more efficiently samples the smaller size classes. This selection may be the result of avoidance of the wheel by the larger and more powerful fish, or the larger and more powerful fish may actually ascend the river in the swifter and deeper water in proportionately greater numbers than the smaller fish which may hug the shores where the current velocity is somewhat less.

A separate experiment was performed in 1958 and again in 1959 in an attempt to determine the susceptibility of the various species and size classes to capture and recapture by the fishwheel. The data of Table 2 show that the chinooks and cohos were least susceptible to recapture by the wheel, while pinks were the most easily recaptured.

A number of fish were recaptured by gillnetters in Taku Inlet each year after they had already ascended the river to Canyon Island, been captured by the fishwheel, tagged, and released. This fishery is centered 25–30 miles from Canyon Island. In 1958 a total of 15 tagged fish or 0.62 percent of fish marked (all species included) were later taken by the gill-net fishery. In 1959, 31 tagged fish or 0.72 percent were taken by the gill-net fishery.

A rapid rise in water level and its associated turbidity causes a general slowing down of the upstream migration of salmon in the Taku which is reflected by the fishwheel catch (Alaska Department of Fisheries, 1952). Figure 4 shows this effect on the pink salmon fishwheel catch in 1952 at Canyon Island.

DISCUSSION

These data show that the fishwheel can be a useful tool in the management of salmon runs, not necessarily as a definitive measurement of the escapement of all size classes of all species but as an index of the magnitude of the escapement. It is quite possible that in many rivers the bias of the wheel will be constant from year to year and hence can be taken into consideration when measuring the escapement. In some cases the combined use of a fishwheel and other gear such as various-sized gill nets might be a practical answer to the accurate measurement of escapement. The individual physical conditions encountered in a particular river system will undoubtedly play an important role in determining the best methods for operating a fishwheel and other companion sampling gear in that system.

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A Method of Estimating Maximum Temperatures to be Expected in Ponds and Small Lakes

Research in methods of measuring evaporation losses from lakes and reservoirs during recent years has provided much information concerning the relation between the thermal

structures of lakes and certain hydrologic and meteorologic parameters. Two theories that have been investigated are (1) the mass-transfer theory, in which the exchange of water vapor between a water surface and the atmosphere is calculated from meteorologic data, and (2) the energy-budget theory, in which an accounting is kept of incoming and outgoing energy, the difference being that available for evaporation. Reports on these studies have been published (U. S. Geological Survey, 1954; Harbeck *et al.*, 1958), but a discussion of the theories is beyond the scope of this paper. The energy-budget theory is rigorously correct, however, and the equation to be presented herein applies to both large lakes and small ponds, subject only to errors resulting from the simplifying assumptions used.

The problem of predicting water temperatures has been studied by other investigators, among them Sette (1940), who estimated the temperatures to be expected in Shasta Reservoir in California on the basis of an analysis of the relation between water and air temperatures at Lake Mead, in Arizona-Nevada, both of which are large reservoirs. A more recent study made by Timofeyev (1958) was based upon energy-budget theory, but he ignored inflow and outflow volumes and temperatures, which the following analysis takes into account.

The incoming radiation or energy supply for a pond consists of both solar radiation (short wave) and atmospheric radiation (long wave). Only a small part of the incoming radiation is reflected by the water surface. Most of it is absorbed and then returned to the atmosphere as back radiation from the water surface. Some energy is utilized for evaporation, and some is transferred to the atmosphere by conduction. Although solar radiation is recorded at many U. S. Weather Bureau stations, atmospheric radiation has been recorded continuously in the United States at very few places.

Available data from six lakes and reservoirs in Texas, Oklahoma, Colorado, Arizona, and California indicated that during summer the net incoming radiation,[1] both atmospheric and solar, was approximately twice the solar radiation alone. Back radiation from the water surface, another item in the energy-budget equation, is proportional to the fourth power of the absolute temperature of the water surface. For simplification the exact relationship was replaced by a linear approximation with a maximum error of 1 percent in the range of water surface temperature normally found in the summer. The energy used for evaporation and the energy exchange by conduction between the water surface and the atmosphere are taken into account by utilizing mass-transfer theory and the Bowen ratio (U. S. Geological Survey, 1954). It is assumed that the change in heat storage in the body of water is zero. Although the change in heat storage even in large reservoirs is usually least at the time of occurrence of maximum surface temperatures, the possible error resulting from the assumption of no change in heat storage is minimized by restricting the use of the equation to lakes or ponds no deeper than 15 or 20 feet, so that the following discussion applies specifically to such bodies of water.

Using the above relations and with certain other simplifying assumptions, the following equation has been developed:

$$Q - 3T_w - 1.3u(e_w - e_a) - 0.4u(T_w - T_a) + 17\frac{I}{A}(T_i - T_w) = 216 \quad (1)$$

in which

Q = incoming solar radiation in langleys (calories per square centimeter) per day
T_w = water surface temperature in °F.
u = wind speed in miles per hour
e_w = vapor pressure of saturated air at the temperature of the water surface, in millibars
e_a = vapor pressure of the air in millibars
T_a = temperature of the air in °F.
I = inflow in cubic feet per second
A = surface area of the pond in acres
T_i = temperature of inflow in °F.

It is not practicable to solve equation (1) for T_w directly; it is much simpler to use a "cut-and-try" method, assuming successive values of T_w until the equation balances. The reason for using water-surface temperature in the analysis instead of temperature at some depth will be discussed later.

During the summer the period for which pond temperatures reach a maximum will vary from place to place because of the seasonal variation in the meteorologic and hydrologic variables in equation 1. It is therefore suggested that computations be made for a week in each of the 3 months of June, July,

[1] Incoming solar radiation minus reflected solar radiation plus incoming long-wave radiation from the atmosphere minus reflected long-wave radiation.

TABLE 1.—*Vapor pressure in millibars at various temperatures*

Temperature (°F.)	0	1	2	3	4	5	6	7	8	9
30	—	—	6.1	6.4	6.6	6.9	7.2	7.5	7.8	8.1
40	8.4	8.7	9.1	9.4	9.8	10.2	10.6	11.0	11.4	11.8
50	12.3	12.7	13.2	13.7	14.2	14.8	15.3	15.9	16.5	17.0
60	17.7	18.3	19.0	19.6	20.3	21.1	21.8	22.6	23.4	24.2
70	25.0	25.9	26.8	27.7	28.7	29.6	30.6	31.7	32.7	33.8
80	35.0	36.1	37.3	38.5	39.8	41.1	42.4	43.8	45.2	46.7
90	48.2	49.7	51.3	52.9	54.5	56.2	58.0	59.8	61.6	63.5

and August. Weekly averages of solar radiation, Q, are published by the Weather Bureau in *Climatological Data—National Summary*, and it would appear satisfactory to use the highest weekly average recorded in the last 3 years in each of the 3 months. Although the wind speed, u, can be obtained from Weather Bureau records at the nearest station, the equation is quite sensitive to the figure of wind speed used, and it would be better to measure wind speed at the site. A totalizing anemometer can be mounted 6 to 10 feet above ground in an unobstructed area and the dials read weekly during hot periods in the summer. The saturation vapor pressure, e_w, is obtained from Table 1 using the assumed value of T_w. The vapor pressure of the air is obtained from Table 1 also, using the dew point of the air, which can be had from Weather Bureau records.

Records of streamflow, which are obtained at thousands of gaging stations located throughout the country, are published by the U. S. Geological Survey and should be helpful in estimating inflow volumes. District offices of this agency can usually provide estimates of minimum flows to be expected during summer months at points where records of streamflow are not available. If possible, inflow temperatures and volumes should be measured during a nonrainy period in the summer.

The air temperature, T_a, can be obtained from Weather Bureau records, adjusted if advisable for local conditions. If the pond is considerably higher in elevation than the weather station, the records can be adjusted approximately by assuming that air temperature decreases about 5½° F. for each 1,000 feet rise in elevation.

Let it be assumed that the following data are available:

July solar radiation, Q, 560 langleys per day
wind speed, u, 3.8 miles per hour
average daily air temperature, T_a, 75° F.
average daily dew-point temperature 67° F.
inflow, I, 0.8 c.f.s.
inflow temperature, T_i, 68° F.
surface area of pond, A, 10 acres

For an assumed water-surface temperature of 81° F., the computations are as follows: from Table 1, e_w is 36.1 mb for a water surface temperature of 81°. Also from Table 1, e_a is 22.6 mb for a dew-point temperature of 67° F. Substituting in equation 1, we have

$$560 - 3(81) - 1.3(3.8)(36.1 - 22.6) - 0.4(3.8)(81 - 75) + 17(0.8/10) \cdot (68 - 81) = 216$$

$$560 - 243 - 67 - 9 - 18 = 216$$

$$223 \doteq 216.$$

If we use a water-surface temperature of 82° F., the left side of the equation becomes 211, so that the equation will balance exactly at a water-surface temperature between 81° and 82°.

Let us now assume that this temperature is higher than is desirable. The meteorologic conditions cannot be changed, but equation 1 can be rearranged to compute the maximum pond surface area that can be provided if the water temperature must not exceed some predetermined temperature, as follows:

$$A = \frac{17\,I(T_i - T_w)}{216 - Q + 3T_w + 1.3u(e_w - e_a) + 0.4u(T_w - T_a)} \qquad (2)$$

Let us assume that the maximum temperature may not exceed 70° F. Substituting in equation 2, we have

$$A = \frac{17(0.8)(68-70)}{216 - 560 + 210 + 1.3(3.8)(25.0 - 22.6) + 0.4(3.8)(70 - 75)}$$

$$= \frac{-27}{216 - 560 + 210 + 12 - 8} = \frac{-27}{-130}$$

$$= 0.2 \text{ acre.}$$

It should be recognized that equation 1 gives results that are conservative, *i.e.*, computed temperatures are generally higher than will be observed at the water surface. Surface temperatures are often, but not always, higher than those observed below the surface. For example, data obtained at Lake Hefner, Oklahoma, in July 1958, show that the reservoir was isothermal throughout the top 30 feet, while the water-surface temperature of a small pond in Texas in August 1958 was 24° F. higher than the bottom temperature at a depth of 20 feet. The principal cause of mixing at Lake Hefner is wind, and if a small pond is well sheltered by surrounding hills or trees, a considerable decrease in temperature with depth may be expected. The foregoing examples are not unusual, but it appears advisable for design purposes to assume that the pond will be isothermal.

The effect of other assumptions used in deriving equation 1 on the computed temperature should be mentioned. It was assumed that the change in the amount of energy stored in the pond was zero. This assumption is on the conservative side also, for during a hot summer week, some of the incoming energy will be used in raising the average temperature of the pond, so that computed water-surface temperatures will be somewhat greater than those observed. During a subsequent cool period, observed water-surface temperature will be greater than computed, but this is of little consequence because maximum temperatures during hot spells are the limiting factor. Another assumption is that the outflow temperature is the same as the water-surface temperature. For ponds having a concrete overflow dam over which a thin sheet of water is constantly spilling, the assumption is reasonable. If water is withdrawn below the thermocline in a stratified lake, the term $(T_i - T_w)$ should be modified by substituting an estimated outflow temperature for T_w. It is also assumed that inflow equals outflow. If outflow during a critical period should be zero, T_w in the term $(T_i - T_w)$ should be deleted.

Equation 1 is admittedly only approximate, but provides a method of estimating pond water temperatures with reasonable accuracy from climatologic and hydraulic data. It is essential that a reliable estimate of wind speed be obtained. The errors inherent in the method are believed to be on the safe side, and the formula should give estimated water temperatures equal to or greater than those observed.

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Tagging of Great Barracuda, *Sphyraena barracuda* (Walbaum)[1]

Although the great barracuda (*Sphyraena barracuda*) is common throughout the coastal waters of Florida, its center of abundance in the State is along the southern portion of the coast. Because it is very abundant, is readily available to both inshore and offshore fishermen, has good fighting qualities, and usually has fine eating qualities,[2] the species is much sought by sport fishermen. It is essentially neglected by commercial fishermen because its habitat preferences in southern Florida (reefs, wrecks, mangroves, rocks) prevent the use of nets for its large-scale procurement. Some landings are reported in the commercial catch, but a large percentage of these is probably the result of sales of sport-fishing catches. Landings reported in 1958[3] and 1959[4] were

[1] Florida State Board of Conservation Marine Laboratory, Contribution No. 53.

[2] The flesh of barracuda, especially large individuals from south Florida, occasionally is known to cause ciguatera. (De Sylva, D. P. (1956) Poisoning by barracuda and other fishes. Univ. Miami Marine Lab., Spec. Serv. Bull. 13, 9 pp., Mimeo.)

[3] Rosen, A. (1959) Summary of Florida commercial marine landings and an analysis of the catch and effort of certain species, 1958. Univ. Miami Marine Lab. 59-4, 55 pp. (Mimeo.)

[4] Rosen, A. (1960) Summary of Florida commercial marine landings, 1959, and an analysis of the catch and effort of certain species. Univ. Miami Marine Lab. 60-2, 53 pp. (Mimeo.)

TABLE 1.—*Length-frequency distributions by 100-millimeter total length classes of dart-tagged barracuda in various months, 1960*

[Tag returns in parentheses]

Month	Length class						Total
	200–299	300	400	500	600	700	
March	2	18	7	4 (1)	1	–	32 (1)
April	–	2	4 (1)	4	3	1	14 (1)
May	–	6	12	4	–	–	22
June	–	20	12 (1)	–	–	–	32 (1)
Total	2	46	35 (2)	12 (1)	4	1	100 (3)

14,547 and 9,892 pounds respectively. These small landings demonstrate the lack of importance of barracuda to the commercial fishery.

Tagging studies on barracuda were begun in March 1960 as part of the State Board of Conservation's program to learn more about the habits and biology of reef and associated fishes. The present paper is essentially a progress report which we feel is warranted since the program was terminated in January 1961. Tag returns are reported through August 15, 1961.

FISHING AREAS, METHODS, AND RECORDS

All specimens were caught by trolling off Key Largo, Florida Keys, except for four seined specimens tagged at Long Key, Florida Keys, and six specimens, two speared and four by casting, caught over a wreck 9 miles west of St. Petersburg, Florida. All locations in the Florida Keys mentioned in this paper are recorded on C. & G. S. charts 1249 and 1250, except for Newport which is the first cutback immediately south of Julia Island, Key Largo.

Usually a single fishing rod, rarely two, was used. A tandem three-hook rig with about 2 feet of leader was tied to the line and baited with a strip of mullet containing a portion of the tail. After the study had been in progress for several months a weighted yellow jig was added to this rig anterior to the hooks. On infrequent occasions spoons or live fish were used for bait, the former with little and the latter with considerable success. Most of the trolling was at speeds of about 1 to 3 knots, but during the last 4 months of the study we found that doubling or tripling this speed seemed to increase the catch.

Measurements were made in millimeters on a standard fish measuring board. Total length, from tip of the protruding lower jaw to the tip of the slightly depressed upper caudal lobe was taken. Only one specimen was caught which showed evidence of damage to the caudal fin. Contrary to popular conception, the barracuda is not a dangerous fish to handle when it is out of water. In spite of considerable threshing one never attempted to bite, and we frequently held the head while tagging.

Records of fishing effort were not begun until November, but based on these it is estimated that there was an over-all average of about 4 or 5 hours of fishing per day (daylight hours only) from 2 to 10 days per month. The catch averaged from about 3 (April) to 11 (May) barracuda caught per day.

TAGS AND TAG RETURNS

The tags and tagging program were advertised over radio, television, in the newspapers, and by posting of placards in fish camps. A $1 reward was offered for each tag returned

TABLE 2.—*Length-frequency distributions by 100-millimeter total length classes of barracuda tagged with Petersen discs, March 1960–January 1961*

[Returns in a particular class in parentheses]

Month	Length class										Total
	300–399	400	500	600	700	800	900	1,000	1,100	1,200	
March	2	–	–	–	–	–	–	–	–	–	2
April	–	–	–	–	2	–	–	–	–	–	2
May	–	3	22 (2)	8 (1)	5	5 (1)	2	1	–	–	46 (4)
June	–	14 (1)	12 (1)	16 (3)	6	2	2 (1)	2 (1)	1	1	56 (7)
July	3	14 (1)	8	2	1	3	–	–	1	–	32 (1)
August	9	15	4	6	3 (1)	1					38 (1)
September	5	9	–	–	–	–	–	–	–	–	14
October	9	32	12 (2)	11 (3)	9	7 (2)	3	2	1 (1)	–	86 (8)
November	14	18 (3)	5	4	–	2 (1)	1	2	1	–	47 (4)
December[1]	–	4	5	5	1	3	5	1 (1)	1	–	25 (1)
January	–	2	4 (1)	5 (2)	3	3	4 (1)	1	2	–	24 (4)
Total	42	111 (5)	72 (6)	57 (9)	30 (1)	26 (4)	17 (2)	9 (2)	7 (1)	1	372 (30)

[1] After November fish less than 450 millimeters total length were not tagged.

TABLE 3.—*Summary of tag returns, March 1960–January 1961*

[Elapsed days include day tagged and day returned]

Type tag	Date tagged	Elapsed days before return	Total length at tagging (mm)	Location tagged	Location caught	Net estimated movement
Dart	March 11	66	579	Julia Is.	Julia Is.	Insignificant
Dart	April 19	23	468	Julia Is.	Julia Is.	Insignificant
Disc	May 11	39	811	Julia Is.	North Key Largo	Less than 5 mi. north
Disc	May 12	32	505	Julia Is.	Julia Is.	Insignificant
Disc	May 15	32	631	Julia Is.	Julia Is.	Insignificant
Disc	June 9	48	610	Julia Is.	4 mi. E. Julia Is.	4 mi. east
Dart	June 9	5	407	Julia Is.	Julia Is.	Insignificant
Disc	June 12	24	652	Julia Is.	Inshore of Rodriguez Is.	Insignificant
Disc	June 13	20	623	Julia Is.	Julia Is.	Insignificant
Disc	June 16	74	536	Julia Is.	Julia Is.	Insignificant
Disc	June 18	8	934	Rodriguez Is.	Carysfort Reef	15 mi. north
Disc	June 18	23	499	Rodriguez Is.	Rodriguez Is.	Insignificant
Disc	June 27	13	1,083	Times Square[1]	Times Square	Insignificant
Disc	July 13	29	405	Julia Is.	Julia Is.	Insignificant
Disc	October 12	18	638	Mosquito Bank	Carysfort Reef	10 mi. north
Disc	October 13	4	814	Molasses Reef	Molasses Reef	Insignificant
Disc	October 13	10	629	Molasses Reef	Molasses Reef	Insignificant
Disc	October 18	6	1,107	Elbow Lt.	Gulf Stream off Carysfort Reef	20 mi. north
Disc	November 10	19	879	Molasses Reef	Marathon off Key Colony Beach	50 mi. southwest
Disc	May 12	224	581	Julia Is.	Julia Is.	Insignificant
Disc	October 13	93	822	Julia Is.	Turtle Reef	15 mi. northeast
Disc	November 8	88	443	Newport	Newport	Insignificant
Disc	November 9	41	456	Rodriguez Is.	Rock Harbor	Insignificant
Disc	November 12	47	404	Newport	Rock Harbor	Insignificant
Disc	December 6	90	1,049	Molasses Reef	Palm Beach	120 mi. northeast
Disc	January 14	4	645	Molasses Reef	Molasses Reef	Insignificant
Disc	January 14	5	579	Molasses Reef	Molasses Reef	Insignificant
Disc	January 16	49	658	Julia Is.	Julia Is.	Insignificant
Disc	October 18	239	593	Basin Hill Shoal	Basin Hill Shoal	Insignificant
Disc	October 18	229	692	Basin Hill Shoal	Basin Hill Shoal	Insignificant
Disc	October 18	215	592	Basin Hill Shoal	Tavernier Creek	18 mi. southwest
Disc	January 14	85	921	Molasses Reef	Whale Harbor	14 mi. southwest
Disc	August 11	340	782	Mosquito Bank	Molasses Reef	4 mi. southeast

[1] Wreck at a depth of 32 feet, 9 miles off St. Petersburg, Florida.

with the requested information (date, location, and total length of fish).

Two types of tags were employed, yellow darts (Everhart and Rupp, 1960) and green plastic Petersen discs with nickel pins.

The dart tag bore the inscription "Fla Bd Cons" and an identifying number. One hundred barracuda were tagged in the muscles of the back just below the anterior dorsal fin with darts (Table 1). The use of darts was discontinued in June after it was found that frequently a tag would fall off before a specimen was returned to the water. Three returns were obtained (Table 3), but we caught them all. The oldest tag, 66 days, was obscured by heavy algal growth. A fourth return was reported to us, but the fish and tag were both lost before we were able to obtain them. Pre-

TABLE 4.—*Sizes (total length in millimeters) of barracuda caught in different habitats, March 1960–January 1961*

Month	Habitat								
	Mangrove			Inshore reefs			Offshore reefs		
	Number	Length		Number	Length		Number	Length	
		Range	Average		Range	Average		Range	Average
March	30	311– 580	409	—	—	—	—	—	—
April	15	314– 786	545	—	—	—	1	682–	—
May	67	333–1,026	565	—	—	—	1	657–	—
June	81	317– 934	499	—	—	—	10	629–1,203	908
July	23	373– 970	494	8	471–1,117	563	1	780–	—
August	22	357– 603	431	13	387– 782	568	3	466– 849	674
September	14	322– 479	407	—	—	—	—	—	—
October	14	363– 822	510	57	328– 967	519	12	414–1,107	803
November	31	302– 699	428	9	338–1,136	569	7	601–1,048	848
December	17	399– 796	524	1	474–	—	12	621–1,049	892
January	14	303– 671	460	1	522–	—	16	487–1,126	791

sumably, an additional disadvantage of the dart is the lack of sufficient space for a legend which will give the fishermen complete instructions on what to do with the tag.

The Petersen tags consisted of two green discs 17 millimeters in diameter. One of the discs of each pair was blank, and the other bore an identifying number on one side and complete information on what to do with the tag and fish on the other. The word "Reward" was also included. Of the 372 barracuda marked with Petersen discs (Table 2) most were tagged in the muscles of the back just below the anterior portion of the second dorsal fin. Others were tagged at positions between this point and the caudal peduncle. The time taken to apply a Petersen tag ranged from 36 to 236 seconds and depended on the size of the fish, how badly it was hooked, and how much it threshed.

Thirty tags (8.1 percent) have been returned (Table 2). On the basis of these short-term returns the disc tag is considered to be reasonably satisfactory for use on barracuda. It seems evident, however, from the lack of returns in the 300-millimeter class that the tags should not be used on specimens below 400 millimeters total length. Returns based only on specimens of the 400-millimeter class and larger would be 9.1 percent of the total tagged (330). During December and January barracuda below 450 millimeters were not tagged because it was not believed that the potential results warranted it. The five returns, 4.5 percent, from the 400-millimeter class are somewhat lower than were expected, but in time this rate of return may improve.

Tag returns are reported in Table 3. Twenty-two specimens ranging in size from 404–1,083 millimeters (average, 586 millimeters) showed insignificant net movement. They were at large from 4 to 239 days (average, 58 days). Eight specimens ranging in size from 592–1,107 millimeters (average, 831 millimeters) showed net movement of from 4–120 miles. They were at large from 6–340 days (average, 87 days). From these meager data it would appear that only fairly large barracuda move any long distance.

ECOLOGICAL NOTES

In Table 4 sizes of barracuda in the three types of habitats fished have been plotted. The inshore reefs are approximately 3 miles offshore, and the offshore reefs are about 6 miles offshore. Tabulations indicate that the average size of barracuda increases as distance offshore increases.

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A Technique for Direct Photography of Translucent Objects[1]

The method described below was developed to demonstrate annuli in otoliths of various serranid fishes in which the age or number of rings is large. It is believed that the method might have wider application.

Otoliths were brushed vigorously with a detergent solution and placed in glycerin for clearing. The otolith was placed on a transparent specimen platform (Figure 1) consisting of a black plastic jar top with a circular hole cut in it and cemented to a 9-inch square transparent plastic sheet (less than 1 millimeter thick). The jar top was filled with sufficient glycerin to immerse the specimen and then placed on a photographic enlarger stage. The stage was then raised or lowered to attain the desired magnification and adjustment made to focus the specimen on an enlarging easel. Any type photographic en-

[1] Contribution No. 57.

FIGURE 1.—Transparent specimen platform displaying affixed jar top.

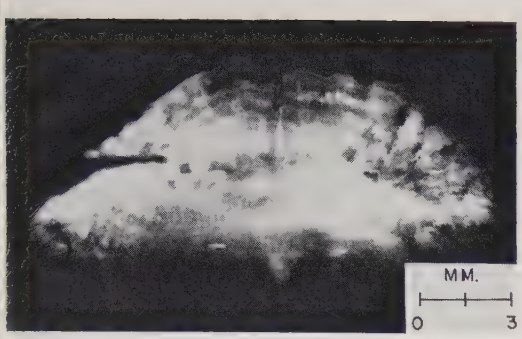

FIGURE 2. — Otolith of *Epinephelus morio* — 5+ years old. Cleared in glycerin for 28 days.

larger can be used for this projection, but in the present case a Simmon Omega with proper condenser and lens for 35-millimeter film was used. This arrangement permitted a larger projected image at a given enlarging position than the condenser and lens for larger film sizes.

The image was projected directly onto F-5 Kodabromide printing paper which was developed in Dektol, washed in a weak acetic acid solution, fixed, and washed for 1 hour. In order to obtain a moderate depth of field with specimens 1 to 2 millimeters thick, a lens aperture of f 10 was adopted as standard. An exposure time of 35 seconds for younger, thinner otoliths and as long as 70 seconds for older, thicker structures was required. More contrast was obtained in developing by decreasing the 2:1 suggested ratio of water to Dektol. Essentially, the picture represents a negative image (Figure 2). Contrast is increased by printing directly so that no intermediate transfers to film are involved. The use of direct light through the structure rather than reflected light increased contrast. Apparent sharpness is gained through increased contrast and by the absence of grain, which is a problem when 35-millimeter film is used. One disadvantage of the method is that no permanent negative is produced; however, by saving the specimen, pictures can be made quickly at any time.

The chief advantages of this technique are that it obviates the use of camera and film and permits rapid photography of a series of specimens of known quality. The chief disadvantage is that the method is limited to relatively thin and/or transparent specimens.

Dr. Shoemaker of the Rochester Institute of Technology (personal communication) suggested exposing the image on the enlarging easel to a negative emulsion so that one might have a permanent negative. Such a procedure would increase the time required and contrast might be lost using a film base unless a high contrast developer such as D-19, made especially for scientific and technical work, is used.

ACKNOWLEDGMENTS

We gratefully acknowledge the aid of G. K. Reid, Florida Presbyterian College, who read and criticized this note. W. S. Shoemaker contributed suggestions and encouraged the authors.

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REVIEWS

ANIMAL SOUNDS AND COMMUNICATION. *Edited by W. E. Lanyon and W. N. Tavolga. (American Institute of Biological Sciences, Publication No. 7.) American Institute of Biological Sciences, Washington. 1960. 443 pp., figs., tables. 12-inch LP record included with volume. $9.50.*

This book is a compilation of the proceedings of a symposium held at the AIBS meetings at Bloomington, Indiana, in September 1958. It is accompanied by a 12-inch long-playing record prepared from a tape recording that accompanied the papers at the Indiana meeting. The table of contents lists nine chapters, or papers, not including the introduction by Dr. J. T. Emlen, Jr., who organized the symposium.

The initial chapter, *Considerations and Techniques in Recording Sound for Bio-Acoustics Studies* by Dr. P. P. Kellogg, should be valuable for anyone contemplating such a study. It is followed by a short paper, *The Analysis of Animal Sounds*, by Dr. D. J. Borror. Chapter Three, *Sound Communication in Orthoptera and Cicadidae*, is written by Dr. R. D. Alexander. Dr. W. N. Tavolga's contribution is entitled *Sound Production and Underwater Communication in Fishes*. Dr. C. M. Bogert has contributed *The Influence of Sound on the Behavior of Amphibians and Reptiles*. Bird sounds are treated in two chapters, *The Ontogeny of Vocalizations in Birds* by Dr. W. E. Lanyon and *Bird Songs and Mate Selection* by Dr. P. Marler. Dr. N. E. Collias has written one of the concluding chapters entitled *An Ecological and Functional Classification of Animal Sounds*, while Dr. C. F. Hackett brings the volume to an orderly conclusion with *Logical Considerations in the Study of Animal Communications*.

It will be immediately apparent to the reader that not all of the animal groups discussed in the book are given similar treatment. Some are discussed mainly from the viewpoint of the author's own research, while others have attempted to bring together all of the available literature pertaining to the group under discussion. Some of the chapter titles may be misleading. For example, Dr. Bogert's chapter, *The Influence of Sound on the Behavior of Amphibians and Reptiles*, contains 167 pages of which only three have to do with reptiles, and here his concern is mainly with sound production rather than with its influence on behavior.

The chapter on *Sound Production and Underwater Communication in Fishes* by William N. Tavolga should be of interest to fishery biologists. Dr. Tavolga discusses various types of sound production and sound-producing mechanisms in fishes, and from each of these types he has chosen examples for further discussion. Recordings of these sounds appear on the record which accompanies the volume, and the results of the spectrographic analyses appear in the text. He also discusses the problems involved with attempts to classify fish sounds on the basis of the morphology of the sound-producing organ ("eventually becomes a listing of sound-producing organs"), on a functional basis, which includes descriptions of the sounds, including frequency range, harmonic analysis, intensity, etc. (". . . has no relationship to the phylogenetic or behavioral aspects of the sound. There is a correlation, however, with the structure of the sonic organs."), and on a behavioral basis (". . . lack of sufficient information on the relationship of fish sounds to behavior"). This is an interesting and well-written chapter and is alone sufficient reason for a fishery scientist to purchase the book.

This book treats a field which is developing rapidly and in which little information is available in a compact source such as this. In the reviewer's opinion this is a valuable and timely work and is deserving of space on every biologist's bookshelf.

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THE BIOLOGY OF MARINE ANIMALS. *By J. A. Colin Nicol. Interscience Publishers, Inc., New York. 1960. 707 pp., figs., tables. $14.00.*

All too frequently scientific books are published having resounding titles, promising much, yet seldom fulfilling expectations. *The Biology of Marine Animals* by J. A. Colin Nicol, Zoologist at the Plymouth Laboratory of the Marine Biological Association, is an exception. In this publication the author presents in clear, concise language on a comparative basis, major physiological activities of different sea animals from the invertebrates to the mammals. Numerous illustrations and tables contribute further to the lucidity of the text.

The book is divided into 15 chapters, an appendix, and index. Chapters cover the subjects of water, salts, and minerals; body fluids and circulation; respiration; nutrition and feeding mechanisms; digestion; excretion; sensory organs and reception; effector mechanisms; nervous system and behavior; pigments and colors; color changes; luminescence; associations; and skeletons, shelters, and special defenses. Subject material is effectively documented by an extensive bibliography at the end of each chapter.

There is little purpose in commenting on individual portions of the text. Nicol's work is stimulating, both in content and method of presentation, and should prove a catalyst to research. The imaginative marine fishery scientist will find in it not only summated information on marine animals but also suggestions for exciting lines of research.

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THE PHYSIOLOGY OF CRUSTACEA. *Edited by Talbot H. Waterman. Vol. 2, Sense Organs, Integration, and Behavior. Academic Press, New York. 1961. 681 pp., figs., tables. $23.00.*

The appearance of the second volume completes the treatise on crustacean physiology. Although intended as a companion to the first, the second book is a coherent unit by itself. In view of the time required for publication of such a text, the information is as up to date as possible. However, since the book went to press, significant contributions have

been made to some of the subjects treated. Such a situation is unavoidable. In anticipation of a constant need for revision the editor wrote, "it is pleasantly stimulating because it shows how lively current interest is in crustacean physiology."

The specific subject matter deals with light sensitivity and vision, mechanoreception, chemoreception and thermoreception, pigmentary effectors, light production, the neuromuscular system, reflexes and the central nervous system, neurohumors and neurosecretion, locomotion, kinetic and tactic responses, physiological rhythms, migrations, and complex behavior. The chapter on light sensitivity and vision by Waterman contains more references (236) than any other.

The final chapter, written by the editor, is an excellent general review of the material covered in both volumes as well as a unique discourse on the nature of comparative physiology. Comparative physiology is defined in general terms as "that kind of physiology in which dependent biological variables are systematized in relation to independent biological variables and in which the causal explanations proposed for these relations rest on biological hypotheses." The important part of this definition is that comparative physiology is characterized by the fact that its independent variables have a biological nature rather than the chemical or physical parameters used in general physiology. For example, a comparative physiologist would determine the relative degree of endocrine versus nervous regulation of chromatophores in a variety of animal species. In this example, the different species would represent the independent variable. The final chapter should be read by all biologists, biochemists, and biophysicists, no matter what their research interest.

Examples of some of the useful tables are: types and distribution of eyes, field observations on the vertical migrations of Crustacea, diurnally rhythmic movements of retinal pigments, solubilities and chromatophorotropic activities of eyestalk extracts, and acetylcholine content of various tissues. Among the original figures are those depicting the possible phylogeny of the Crustacea and the structures of decapod compound eyes.

The indexes are as extensive as in the first volume. An author index indicates the page on which the individual's work is mentioned and the page on which the bibliographic citation occurs. A systematic index includes the current valid name of each organism as used in the text plus names that have been superseded but were used by the investigators cited in the bibliography. Included as an aid in using the systematic index is a synopsis of crustacean classification extracted from Chapter 1, Volume 1. The subject index, 45 pages, is also very good.

The editorial level is excellent. Only six typographical errors were noted. Numerous cross references between chapters contribute significantly to the value of the volume. Very little overlap of information occurs between chapters. Some overlap, however, is unavoidable in a work of this sort. In some chapters the reader becomes bogged down by the mass of data. However, the summary at the end of each chapter helps tie together the loose details.

In short, in the opinion of the reviewer, this volume is indispensable for an investigator of the comparative physiology of Crustacea.

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Guide to Marine Fishes. *By Alfred Perlmutter. New York University Press, New York. 1961. 431 pp., figs. $6.50.*

The author states, "The species included in this guide are all of the marine fishes and fish-like vertebrates commonly found along the shores of the temperate-water zone from Cape Cod to Cape Hatteras, together with some of the more common stragglers from the regions north of Cape Cod and south of Cape Hatteras and from the deep waters offshore." The book is addressed to the layman.

Approximately 250 species are included in an illustrated key. In a separate section of the book an outline drawing is given of each species along with a brief discussion which includes, for most species, paragraphs on color, distribution, size, general information, and economic importance. Brief sections on characters, general information, economic importance, and classification are given for the sharks; sawfishes, skates, and rays; and true fishes.

The key in this book is said to represent "a new method for identification of marine fishes." This method consists of placing all of the species in a single, large, artificial key which uses external characters. Although some closely related genera are placed far apart in the key, closely related species are generally placed together, and the characters used to distinguish them are in many instances the old, tried, and unfortunately sometimes untrue ones that date far back into the literature.

Judged from the point of view of its desirability for a lay audience, this book is not ideal. The key is difficult to work with in certain spots. Problems of seasonal variation in distribution are oversimplified or ignored. The author has not followed his own criteria for inclusion of species. About 10 percent of the species included are listed as rare strays and could easily have been omitted. Another fault is the complete absence of references. Any nonbiologist who is interested enough in fishes to pay $6.50 for this volume surely deserves to know where to look for additional information.

Although some of the information in this volume is undoubtedly based upon original observations by the author, lack of documentation reduces the value of the book to a professional biologist seeking help with identification or information on any particular species.

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Efficiency Evaluation—Tracy Fish Collecting Facility, Central Valley Project, California, *by D. W. Bates and others. 1960. 70 pp.*

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